Issued January 13, 1913.

U. S. DEPARTMENT OF AGRICULTURE.

BUREAU OF PLANT INDUSTRY—BULLETIN NO. 256.

B. T. GALLOWAY, *Chief of Bureau.*

HEREDITY AND COTTON BREEDING.

BY

O. F. COOK,

Bionomist in Charge of Crop Acclimatization and Adaptation Investigations.

WASHINGTON:

GOVERNMENT PRINTING OFFICE.

1913.

Issued January 13, 1913.

U. S. DEPARTMENT OF AGRICULTURE.

BUREAU OF PLANT INDUSTRY—BULLETIN NO. 256.

B. T. GALLOWAY, *Chief of Bureau.*

HEREDITY AND COTTON BREEDING.

BY

O. F. COOK,

Bionomist in Charge of Crop Acclimatization and Adaptation Investigations.

WASHINGTON:

GOVERNMENT PRINTING OFFICE.

1913.

BUREAU OF PLANT INDUSTRY.

Chief of Bureau, Beverly T. Galloway.
Assistant Chief of Bureau, William A. Taylor.
Editor, J. E. Rockwell.
Chief Clerk, James E. Jones.

Crop Acclimatization and Adaptation Investigations.

SCIENTIFIC STAFF.

O. F. Cook, *Bionomist in Charge.*

G. N. Collins, *Botanist.*
H. Pittier, *Special Field Agent.*
Albert T. Anders, G. B. Gilbert, J. H. Kinsler, Charles G. Marshall, and D. A. Saunders, *Agents.*
Charles H. Clark, C. B. Doyle, James H. Kempton, and R. M. Meade, *Assistants.*
Robert A. Gorham and Walton G. Wells, *Student Assistants.*

ADDITIONAL COPIES of this publication may be procured from the Superintendent of Documents, Government Printing Office, Washington, D. C., at 15 cents per copy

LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., May 25, 1912.

Sir: I have the honor to transmit herewith a paper entitled "Heredity and Cotton Breeding," by Mr. O. F. Cook, Bionomist in Charge of Crop Acclimatization and Adaptation Investigations, and to recommend its publication as Bulletin No. 256 of the bureau series.

This paper outlines some new methods and standpoints for the study of heredity, with applications to practical problems in the breeding of cotton. It shows how problems of heredity and methods of breeding can be simplified by a more definite recognition of the fact that the expression of characters is distinct from transmission. In addition to these general results detailed information is given regarding the habits of the various types of cotton, the effects of external conditions, and the behavior of the different characters in heredity.

In addition to its use by other investigators and breeders, a general paper of this kind should render the subject of cotton breeding more interesting from the educational standpoint and assist extension workers in understanding and presenting to the farmer the reasons for the improved methods of selection that have been developed. Though the paper necessarily deals with scientific distinctions, technical terms are employed only when the meanings are explained by definitions or by reference to familiar facts.

Very respectfully,

B. T. Galloway,
Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

CONTENTS.

256

ILLUSTRATIONS.

PLATES.

TEXT FIGURES.

B. P. I.—755.

HEREDITY AND COTTON BREEDING.

INTRODUCTION.

The breeding of new varieties is no more difficult with cotton than with other plants, but the relation of heredity to the cotton crop does not end with the breeding of varieties. To preserve a superior variety so that it can be utilized for purposes of production is a more difficult practical problem than the breeding of a new variety, and requires an equally intimate acquaintance with the facts of heredity. On account of the industrial uses of the cotton fiber, uniformity is of much greater importance than with other field crops, but methods that secure uniformity in other crops are not applicable to cotton. The habits of the plant and the unorganized state of the industry seem to preclude the establishment of any centralized system of seed production.

The improvement of the cotton industry through the utilization of superior varieties is likely to require a large development of popular interest in the applications of heredity to cotton production. The methods of scientific agriculture are much more likely to secure effective application among those who understand the underlying facts that make such methods necessary. The farmer who undertakes to follow directions without understanding the reasons for them is likely to make but poor and ineffective use of any method that requires special care or skill.

The intelligent farmer has not only a material advantage to gain but also a much greater interest and satisfaction in his work, if he learns the reasons for what he is doing and is able to place a correct interpretation upon the characters and behavior of the plants that engage his attention. It is true that a special training is necessary for effective work in breeding and selection, in the sense that detailed knowledge is required, but it is a training that can be secured on the farm better than anywhere else. Moreover, the cotton plant affords unusual opportunities for gaining insight into the problems of heredity and breeding. Many of the complicated methods used on other plants by laboratory workers and statistical biologists are unnecessary with cotton, for reasons that are explained in this bulletin.

Direct, practical familiarity with the fact of heredity in such a plant as cotton is a much more effective training in plant breeding than any that the school can supply through the medium of formal instruction. The farmer who learns how to select his own cotton not only makes his crop more profitable but has something of real value to teach his children. In spite of the general tendency to assume that everything in the way of detailed knowledge must be learned in school, the educational possibilities of farm life are beginning to be appreciated. The development of a truly agricultural civilization will be assured when people understand that farm life has larger possibilities of human development than urban existence. Genuine farm education is needed—not merely agricultural courses in schools.

It is not expected that this bulletin can be made generally available for the purpose of home instruction in cotton breeding, nor is it intended for this purpose. Such a manual, containing detailed accounts of the characters and habits of the varieties, might be useful in educational work but is not yet available. The best way to become familiar with a variety of cotton is to study it in the field. Such study is facilitated by having a general point of view for understanding the facts, even more than by being told in advance exactly what should be seen. This bulletin states the general biological reasons for the methods of breeding and selection that have been suggested in previous publications of the Bureau of Plant Industry.[1]

A recognition of the general relations of heredity to cotton breeding is the first requisite for placing the subject on an adequate scientific basis. The real task of agricultural investigators, experiment station workers, and other agencies enlisted in the improvement of the cotton industry is the education of the cotton-growing public, so that better cotton can be grown. But the experts must first understand the problem, if their teaching is to benefit the public.

It is not safe to prescribe methods of cotton breeding merely on a basis of analogy with other crops. The methods developed for cereals and other self-fertilized plants are not adequate. A much wider range of biological facts must be taken into account in the breeding and selection of open-fertilized plants like cotton. Indeed, the problem of preserving and utilizing superior varieties of cotton has important economic and educational aspects, for it can not be solved by the individual farmer working alone, but requires the organization of cotton-growing communities devoted to the produc-

[1] Local Adjustment of Cotton Varieties, Bulletin 159, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909. Cotton Selection on the Farm by the Characters of the Stalks, Leaves, and Bolls, Circular 66, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1910. Cotton Improvement on a Community Basis, Yearbook, U. S. Dept. of Agriculture, for 1911, pp. 397–410.

tion of a single type of cotton. Hence the need of a general statement of the underlying principles or physiological factors of heredity that have to be applied in the breeding and selection of cotton.

Facts of nature have an interest of their own, apart from any general inferences or applications. As Emerson has said, "Nature is loved by what is best in us." But when practical applications are to be made the facts must be interpreted. Investigators of heredity propose to apply their results to the breeding of improved plants and animals, and even to human eugenics. In drawing conclusions for such purposes the utmost caution is required, not only in basing our inferences on large numbers of facts but in distinguishing different kinds of facts and understanding their relations to each other.

Investigating facts from the wrong point of view is like traveling on the wrong road. Instead of bringing us nearer to the end of our journey, the most diligent effort may only expose us to unexpected dangers. To give advice on breeding problems without taking the underlying physiological factors into account is to invite disaster and confusion. Many attempts have been made to establish a distinction between pure science and applied science, the assumption being that more careful or fundamental researches are made when no practical objects are in view. But in reality the most complete and adequate knowledge is required to meet the test of practical application and thus open the way to further progress.

THE NATURE OF HEREDITY.

Heredity, the resemblance of offspring to parents and ancestors, is one of the most familiar facts of nature and yet one of the most mysterious. Nobody has been able to imagine any sort of mechanism that would perform the work of heredity, much less a mechanism of the nature of a fluid jelly, like the protoplasm of the living cell. The first theory of heredity assumed that the new organism was preformed in the egg as a minute model that developed to visible size after fertilization. This notion was long since given up, but the idea of models or other determining mechanisms continues to serve as the basis of speculation regarding the nature of heredity. Though it is no longer expected that the microscope will reveal infinitesimal plants or animals swimming in the protoplasm, the hope is still cherished that something in the protoplasm of germ cells may be found to represent the future organism or at least the component parts or "unit characters" of which the bodies of plants and animals are supposed to be built.

Naegeli found reasons for believing that organic characters must be transmitted by solid particles rather than by liquids or solutions, and the idea of material determinants has been greatly elaborated

by Weismann and his followers. But none of the corpuscular theories thus far proposed can be said to convey an adequate conception of the processes of heredity. Characters can be thought of in other ways more consistent with the facts of heredity.

Many of these speculations regarding the internal mechanism of heredity are interesting, but it has yet to be shown that any basis of fact has been secured or that they have been of real assistance in recognizing or interpreting the external phenomena. The science of heredity is still in the first stage of development. Primary questions regarding the normal conditions and manifestations of heredity are still to be answered. Some of the most general and fundamental facts in organic nature, such as the organization of plants and animals into species, and the individual diversity everywhere found among the members of normal species, are left out of account in current theories of heredity and breeding. Though it is hardly possible to understand the nature of heredity without recognizing the conditions of its normal manifestation, this phase of the subject usually receives little or no attention in our educational institutions. Very few students become familiar with the facts of diversity in natural species or even have the need of such familiarity brought to their attention.

Failure to recognize diversity and free interbreeding among the members of species as normal conditions of organic existence has made it possible to look upon uniform, unchanging "pure lines" of descent as examples of normal heredity. But uniform expression of characters is not the form of heredity shown in natural species where free interbreeding forms a connected fabric of interwoven lines of descent. Such interbreeding maintains the vigor and fertility of the group, but these qualities are lost when descent is restricted to narrow strains or individual lines. The vigor secured by the crossing of different lines of descent ought to be recognized and utilized as a normal factor in the physiology of reproduction, instead of being looked upon as something exceptional and monstrous, like the abnormal phenomena of hybridization. Biological evidence indicates that the general application of pure-line theories to plants and animals, or to mankind, would not bring permanent strength or improvement, but would lead ultimately to weakness and extinction.

The individual diversity of mankind, the most familiar fact of heredity, may be taken as an example of the normal condition of expression of characters in freely interbreeding wild species. To accept uniform expression of characters as the normal state of heredity would amount in the human species to the acceptance of identical twins as typical examples of human inheritance. The usual object of breeding superior varieties of domesticated plants and animals is to produce larger numbers of individuals with the

same set of characters, but this is not assisted by assuming that uniform expression of characters is a normal condition of heredity. If uniformity were the normal condition a selected "pure strain" might be expected to remain uniform, but in reality selection must be maintained or the variety will "run out" by returning to the original condition of diversity.

MATERIALS OF HEREDITY AFFORDED BY THE COTTON PLANT.

The cotton plant affords unusual opportunities for the investigation of problems of heredity. The large size of nearly all the parts greatly facilitates the study of characters and the recognition of variations. The period of flowering is not limited to a few days, but often continues for three months or longer, through the whole period of crop development, so that all of the adult characters can be studied on the same plants at the same time.

The length of the flowering and fruiting season allows the effects of changes of external conditions to become apparent in the different parts of the same plant. Thus, it is possible to learn the extent of the changes that can be brought about, even in the adult plants, by differences of temperature and humidity while the plants remain in the same soil.

The cotton plant has several highly specialized characters that are unusually susceptible of changes in definite ways, whether from genetic or environmental causes. The most specialized features are the two types of branches, different in structure, function, and form of leaves; the double involucre, with two forms of bracts; and the fibrous covering of the seed, with the two types of hairs. The specialized characters are not only more susceptible to the influence of external conditions, but are also most frequently affected by other kinds of variation.[1]

The cotton plant also furnishes an unusual wealth of materials in the way of distinct varietal and specific types. No other genus of crop plants contains so many domesticated species, to say nothing of the endless varietal forms to be found in all cotton-growing countries. While the different types are being compared and tested for cultural and breeding purposes there are ample opportunities for the study of parallel variations and reversions to ancestral characters and of the relation of such variations to differences of external conditions.

[1] Several of the specialized characters of the cotton plant have been described in previous publications of the Bureau of Plant Industry, U. S. Dept. of Agriculture: Bulletin 88, Weevil-Resisting Adaptations of the Cotton Plant, 1906. Bulletin 198, Dimorphic Branches in Tropical Crop Plants: Cotton, Coffee, Cacao, The Central American Rubber Tree, and the Banana, 1911. Bulletin 221, Dimorphic Leaves of Cotton and Allied Plants in Relation to Heredity, 1911. Bulletin 222, Arrangement of Parts in the Cotton Plant, 1911. Bulletin 249, The Branching Habits of Egyptian Cotton, 1912.

In addition to the several distinct species and numerous varieties of cotton in regular commercial cultivation, many unimproved types are scattered through the tropical regions of both hemispheres. Some are in the hands of primitive tropical tribes, while others are still in the wild state. Such materials are needed for the study of heredity, in order to complete the series between normally diverse, unselected species and uniform, line-bred strains, like those that usually figure in laboratory and garden investigations.[1]

Without such comparisons between the behavior of characters in different groups, and the reactions of the same groups to different environments and states of breeding, it is very difficult to learn the expression relations of the different characters or to appreciate the larger relations between heredity and evolution. In the absence of a distinction between uniform pure lines and diverse natural species, any definite change in the expression of a character is likely to be mistaken for an evolutionary development of a new character or a new species, as assumed in the theory of mutation.

The study of cotton, as of many other plants, leaves no doubt that abrupt mutative changes of characters take place and that such changes are often permanent. Some mutations are superior to the parental stocks and are useful as parents of improved strains. Other mutations, and by far the larger number, are inferior and serve to destroy the uniformity of select strains unless recognized and removed. The preservation of uniformity in superior varieties of cotton is only to be accomplished by a vigilant roguing out of inferior mutations.

The same general range of diversity has been found among the members of unselected types of cotton as among the degenerate variations, "sports" or "mutations," that continue to appear in the most uniform strains that have been developed by selection. In the breeding of cotton for weevil resistance and other new requirements it has been necessary to take account of the diversified characteristics of wild species and unimproved stocks that have never been reduced to uniformity by methodical selection.

The fact of mutative change does not prove that the characters of mutations are new or that they represent progressive steps in the evolution of natural species. The wild and unimproved types of cotton are not separated from each other by definite unit-character differences like those that distinguish the mutative variations that appear in otherwise uniform, select strains. That mutations do not

[1] In nature, among open-pollinated (allogamous) plants (and presumably among a great many animals) there is no such thing as a "pure" species which will breed true in all its characters, showing only purely fluctuating variability. It is only by selecting and inbreeding for a few generations that we get "pure lines." The only pure lines in nature are to be found among strictly self-fertilized (autogamous) forms. (See Gates, R. R., "Mutation in Oenothera," American Naturalist, vol. 45, 1911, p. 578.

represent new species is no reason for disregarding their existence, nor for failure to recognize their practical importance.

The methods that have been applied to the study of the cotton plant have been developed through a previous familiarity with similar facts of natural diversity, mutative variation, and definite specialization of vegetative parts in coffee and other crop plants of tropical origin belonging to several different families. Members of many wild species of plants and animals, natives of widely different conditions, tropical and temperate, humid and dry, have been compared and found to represent the same primary condition of individual diversity. Even the wild wheat plant recently discovered by Aaronsohn [1] in Palestine has proved to be a normally diverse interbreeding species, in complete contrast with the uniform self-fertilized strains of domesticated cereals that have figured so largely as the basis of general conclusions regarding the nature of heredity and the principles of breeding.

HEREDITY IN NATURAL SPECIES.

Interpretations that seem to accord very well with one group of facts appear entirely inadequate when put to the test of more general application. Many theories of heredity and evolution deduced from laboratory experiments are fundamentally at variance with conceptions formed by naturalists familiar with species in nature. Natural species seldom show definite character-unit differences like the mutative variations that have been supposed to represent the origination of new characters and new species under experimental conditions. Laboratory experimenters seldom take into account the constitution of natural species. In like manner field naturalists often disregard facts that have been demonstrated by laboratory experiments, being unable to accept theories that have been deduced from such facts.

The present limited views must give place to a conception broad enough to include the facts of heredity shown in large natural groups as well as those ascertained by formal experiments with select individuals or strains. The apparent conflict only shows the need of studying the subject from other standpoints, with no misleading insistence upon one particular kind of facts to the exclusion of other kinds. Nature is a vast experiment where improved methods of reproduction and inheritance of characters are being worked out in the evolution of millions of different species. Evidence is readily had on almost any point, if we only know where to look for it. The

[1] Aaronsohn, A. Agricultural and Botanical Explorations in Palestine. Bulletin 180, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1910, pp. 42–45. In addition to the facts of diversity reported by Aaronsohn, direct evidence of interbreeding was found during a visit to Palestine in the summer of 1910. (See Report of the Acting Chief of the Bureau of Plant Industry for 1910, p. 24.)

conditions of evolutionary progress in nature must be recognized and accepted as a general basis or background for the interpretation of special groups of facts secured by special methods of breeding.

The idea of heredity as a process of segregation or separate transmission of character units derived from different parents does not comport with the general facts of evolution. Species differ from each other and their members differ among themselves in ways that are not recognized from the laboratory point of view. The development of new characters and organs requires the combination and integration of many variations, as provided by the association of plants and animals into specific groups of freely interbreeding individuals. Mutative variations of select stocks should not be confused with the gradual development of new characters in natural species.

Some writers have considered evolution as a process of isolation and segregation of characters, but cases supposed to represent the origination of new species in this way can be better understood as examples of abnormal variations or reversions. With the facts of heredity limited to a few animals and plants bred in cages and gardens, it is possible to entertain the conception that new species arise by sudden changes of unit characters, but those who are familiar with natural species know that they are very differently constituted. An adequate conception of heredity must recognize the conditions of inheritance among the freely interbreeding lines of descent in natural species as well as the conditions found in selected varieties where the natural network of descent has split into narrow strands or individual lines.[1]

The individual plant or animal represents one of the junctions or knots of the network of descent. Vast numbers of lines of descent pass through each joint of the network, lines that converge from all the ancestors and diverge to all the descendants. The fact that organisms lose their vigor and fertility when removed from the network of descent by being propagated in separate lines, but show renewed vitality when the separated lines are reunited, makes it evident that the weaving of the lines together to form a network of descent has a physiological value. Reproduction in a broad network of descent maintains the vigor and fertility of species, while reproduction in single or narrow lines sustains vitality for only limited periods.

Many kinds of plants and animals can be propagated in simple or narrow lines of descent for a series of generations, but there is nothing to indicate that any method of line breeding will permanently maintain the vitality of a stock. If propagation takes place

[1] Cook, O. F. Methods and Causes of Evolution. Bulletin 136, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1908. See also "The Superiority of Line Breeding over Narrow Breeding," Bulletin 146, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1909.

by self-fertilization or some other form of line breeding, uniform expression of characters may become established in natural species, the same as in pure lines that are artificially bred, though in nature such lines are only temporarily separated from the network of descent of the species. The normal evolutionary species is represented by the network of diverse interbreeding lines, not by the uniform self-fertilized lines. Self-fertilization, parthenogenesis, and vegetative propagation are to be considered as supplementing sexual reproduction, not as adequate substitutes for natural crossing of the lines of descent.

The relation of the network of descent of the species to the maintenance of vigor and fertility has become easier to understand in the light of recent discoveries regarding the nature of the cells that compose the bodies of the higher plants and animals. There is a profound difference in this respect between the higher types of organisms and some of the lower groups. The nuclear elements of the cells that compose the bodies of the higher types are double, so that each cell corresponds to two cells in the lower types. This peculiar condition of double cells arises from a difference in the process of conjugation. In the lower groups conjugation is completed in a comparatively brief period of the life history, while in the higher groups the cells remain in the double, conjugating condition during a very large part of the life history, so that it is possible to build up large bodies composed entirely of double cells, representing a state of prolonged conjugation of the original gametes.[1]

SPECIES AS PHYSIOLOGICAL ORGANIZATIONS.

In attempting to understand the structure of protoplasm as a mechanism of descent, the structure of the species as a network of descent has been left out of account. Though the association of organisms into species does not serve structural or economic purposes directly, it has the physiological function of maintaining vigor and fertility. From the physiological standpoint it is just as necessary to recognize the existence of the network of descent of the species with normal diversity and free interbreeding, as to understand the cellular and protoplasmic structure of the bodies of individual plants and animals.

That the individual plant or animal represents a social organization of the various kinds of cells that compose the body is a familiar idea among students of structural biology. Moreover, the individual cells are connected into a network by narrow strands of protoplasm that perforate the walls. Even the protoplasm itself is now known to have a reticular or netlike structure.

[1] Cook, O. F., and Swingle, Walter T. Evolution of Cellular Structures. Bulletin 81, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1905.

More complex types of structural units are found in the segments of animals and the internodes of plants. This is most obvious in cases where the numerous metamers or joints that make up the body are also capable of an independent existence. The different kinds of internode metamers that compose the bodies of plants may be compared also with the several different kinds of specialized individuals found in colonies of social insects—bees, ants, and termites. Though many groups of plants and animals have the power of vegetative or asexual reproduction, none of them have been able to dispense with sexual reproduction. For many agricultural purposes vegetative propagation is superior to sexual reproduction, but vigor and fertility are not permanently maintained.

The specific constitution or speciety of living matter, the association of all plants and animals into normally interbreeding specific groups, should be considered as one of the distinctive biological properties or necessary conditions of the continued existence of complex organisms. The perpetuation of all the higher types of plant and animal life seems to be as truly dependent upon the fact that organisms are always associated in species as upon other properties of protoplasm that are usually recognized, such as irritability, assimilation, growth, and reproduction.

In the study of heredity and breeding, primary consideration should be given to the constitution of natural species as networks of interweaving lines of descent rather than to the formal taxonomic idea that species are based on "identity of form and structure," as a dictionary definition states. The identity sought for by the systematist is in reality merely an agreement in a few formal characters that most readily serve the taxonomic purpose of distinguishing the members of one species from those of another.

This formal taxonomic view of species has often misled evolutionists as well as students of heredity. The subdivision of large species into smaller and more uniform groups does not represent the typical condition of evolutionary progress any more than uniform groups represent the typical condition of heredity. Evolutionary progress is represented by changes of characters in large species rather than by the isolation of numerous small species. Heredity, no less than evolution, is a group phenomenon. The specific network of descent rather than the individual line is the fundamental fact of heredity, as of evolution. Not to know the constitution of the species is not to understand the constitution of the germ cell, for the one depends on the other.

The differences found among the members of one large species are often greater than those that serve to separate smaller or more uniform species. The diversity of large species is the most favorable condition for evolutionary progress, as Darwin recognized, and it

also represents the typical condition of heredity and breeding. The diversity found in the human species, for example, is more normal than the uniformity of "pure strains" of domesticated plants and animals. The development of a uniform "pure strain" of a domesticated plant or animal is an agricultural improvement when it enables the yield or the commercial value of the product to be increased, but no one who appreciates the biological nature of such strains would propose to use the same methods for the improvement of the human species.

Many of the variations selected as improvements of plants and animals for economic purposes represent negative changes or suppressions of characters. Instead of the total equipment or content of transmission being increased by constructive additions of new characters or functions, the expression of some of the characters is reduced or omitted altogether. It is a mistake to confuse the results of individual selection with the evolution of species through progressive changes of characters under natural conditions of free interbreeding.[1]

Selection regulates the expression of characters by restricting descent to particular lines that show the desired characters or degrees of expression, but there is no reason to believe that new characters not already present in the ancestry of the group can be brought into existence by selection. The most carefully selected types of Upland cotton do not have larger bolls or longer lint than are found in some of the native Central American stocks of Upland cotton that have not been subjected to conscious selection.

TRANSMISSION DISTINCT FROM EXPRESSION.

Two distinct processes are involved in heredity. The transmission of characters is independent of expression. If transmission and expression were the same, the transmission of a character would necessarily involve expression. All the characters would be shown in all the individuals that are able to transmit them. In reality a large part of the characters are transmitted without being brought into expression. They may remain for many generations in a dormant or latent condition. The full series of transmitted characters might be compared to the stock carried by a merchant, while those

[1] "The pure line, while a valuable and necessary means of analyzing various problems of heredity, is essentially a laboratory product seldom duplicated in nature among allogamous plants. By continued inbreeding and selection to smaller and smaller differences, races which are more and more uniform may be obtained, as the 'pure-line' work tends to show. But the natural wild species must (unless regularly self-fertilizing) be looked upon as an intercrossing population of races whose appearance is ever changing (within limits) from generation to generation, according to the particular series of crosses or 'selfings' which happen to occur in each generation. Some of the races are likely to fluctuate in numbers or be dropped out entirely as conditions change." (See Gates, R. R., "Mutation in Oenothera," American Naturalist, vol. 45, 1911, p. 578.)

that are brought into expression would represent the small assortment placed in the show window.

The failure of a character to come into expression is not the same as a failure of transmission, for the character may reappear in later generations. Though all the lines of descent share the same general equipment or content of transmission, each individual is necessarily limited to the expression of a single set of characters. Transmission may be considered as a permanent, invariable factor or common denominator of heredity; expression as a small and highly variable numerator of the individual fraction.[1]

In this conception of a germ cell as a transmitter of all the ancestral characters modern science affords a curious parallel with the ancient allegory of Pandora, the All-Gifted, the woman who received all the good and evil gifts of the gods for mankind. Pandora was blamed for letting the gifts of the evil deities escape into the world, while those of the good deities were left imprisoned. Bringing the wrong characters into expression may still be considered as the chief impediment of human progress. Pandora was married to Reflection, the brother of Progress. The Greeks were in advance of us in appreciating the importance not only of eugenics but of what might be called "euphanics," or the art of bringing desirable qualities into expression. They recognized the need of training the young by intimate contacts with all the activities of life, instead of limiting education to formal instruction in schools.

The breeder, no less than the educator, has to deal with expression of characters. The processes of transmission are still beyond our control, as well as outside our comprehension. The practical problems of heredity lie in the field of expression. The differences that exist among members of the same species, varieties, or strains, the differences that serve as the basis of selection and of all investigations of heredity and breeding, are differences of expression rather than differences of transmission. Selection is our means of avoiding the expression of undesirable characters, but there is no way to exclude them from transmission, except by destroying the whole stock. For constructive progress it is not enough to reject the obviously inferior individuals. Preference must be given not only to the best individuals, but to those that yield offspring without the undesirable characters. The chief problem of heredity is to understand the laws that control the expression of characters.

In a normally diverse wild type each individual shows a different set of characters, a fact most familiar in the human species. Identical twins illustrate the expression of the same set of characters in two individuals. Uniform, selected varieties or "pure strains" of

[1] Cook, O. F. Transmission Inheritance Distinct from Expression Inheritance. Science, n. s., vol. 25, June 7, 1907, p. 911.

domesticated plants and animals represent the expression of the same set of characters in large numbers of individuals, but the usual normal condition is a varied or alternative expression of different sets of characters. In the Mendelian theory of heredity, transmission is supposed to be limited to a single set of characters. Failure to distinguish clearly between transmission and expression is a frequent cause of confusion and ambiguity in the literature of heredity. Many writers identify heredity with transmission, as in the theory of Mendelism, while others use heredity in the sense of expression.[1]

Apart from this misleading assumption, the special study that has been given to Mendelism in the last decade has been of use in bringing alternative phenomena of heredity into greater prominence. Attention has been given almost exclusively to Mendelian forms of diversity, but other phenomena of alternative expression are of more general significance. The result of alternative expression of characters in natural species is to preserve variations and maintain diversity, even under conditions of free interbreeding. Recognition of this fact removes the ground for the former belief that variations could not be preserved and made effective for evolutionary progress unless they were isolated, because of the alleged " swamping effects of intercrossing." The older idea of the results of mixing different species or varieties was that the characters would finally blend or reduce to an intermediate average, but this no longer appears to be true. The distinctive characters of the parental types are not lost or permanently fused in the hybrids, but continue to be capable of full expression in later generations.

Though an intermediate expression of contrasted parental characters often occurs in the first-generation or conjugate hybrids, this is now recognized as a merely temporary condition. In the second-generation or perjugate hybrids the parental characters reappear in fully contrasted expression instead of being limited to intermediate or blended expression as in the first generation.

The theory of alternative transmission may appear adequate as long as the second generation shows nothing outside the range of the parental characters, but when a wider range of diversity is found, as usually happens in cotton hybrids and frequently in the hybrids of other plants, it becomes evident that crossing has done more than to form different combinations of the contrasted parental characters by alternative transmission. Another effect of crossing

[1] " Our second purpose in this Harvey Lecture is to show that the evidence for continuity in the genesis of certain characters in man and other mammals is very strong indeed; further, that some of these characters, while apparently continuous in origin, certainly become discontinuous in heredity; from which it follows that discontinuity in heredity constitutes no proof of discontinuity in origin." (See Osborn, H. F., " The Continuous Origin of Certain Unit Characters as Observed by a Paleontologist," American Naturalist, vol. 46, 1912, p. 186.)

varieties is to arouse latent characters to expression and thus induce a return toward the normal diversity of the species.

Any definite variation that has once occurred in a species is likely to reappear in undiminished form in at least a part of the offspring or their descendants. New variations do not need to be separated from the parent stock by selection or otherwise in order to escape the alleged "swamping" effect of dilution with the parent form. The principle of alternative expression provides for the development of new characters and functions by accumulation and integration of variations or, in other words, by building up advantageous relations of expression among the different alternative characters. The effect of selection is to regulate the expression of characters and establish the more advantageous combinations.

What there may be in the protoplasm of the cells to correspond to the external features of plants and animals and make possible an accurate transmission of such features from one generation to another is not known. Only the results of heredity are definitely known; the mechanism remains a matter of conjecture. The results afford some indications regarding the workings of the process, but these indications are in the nature of inferences, not direct observations. The characters have to be seen and thought of as external appearances, not as internal entities of the protoplasm. The study of heredity is based simply on observation and comparison of individual plants or animals to see whether they are alike or different; in other words, upon the expression of the characters.[1]

VARIATIONS AS CHANGES OF EXPRESSION.

Until the nature of the mechanism of heredity is understood no complete answer can be given to questions regarding the causes of variation. Experiments may prove that the expression of a character is modified by an external condition, but do not show how the internal processes of heredity are affected. For some purposes it is sufficient to say that a certain character is caused or induced by a certain condition, but there may be many untraced steps between the external condition or "cause" and the consequent variation.

[1] "We know already that the experience of the breeder is in no way opposed to the facts of the histologist, but the point at which we shall unite will be found when it is possible to trace in the maturing germ an indication of some character afterwards recognizable in the resulting organism. Till then, in order to pursue directly the course of heredity and variation, it is evident that we must fall back on those tangible manifestations which are to be studied only by field observation and experimental breeding.

"The breeding pen is to us what the test tube is to the chemist—an instrument whereby we examine the nature of our organisms and determine empirically what for brevity I may call their genetic properties. As unorganized substances have their definite properties, so have the several species and varieties which form the materials of our experiments. Every attempt to determine these definite properties contributes immediately to the solution of that problem of problems, the physical constitution of a living organism." (See Bateson, W., "Heredity and Evolution," Popular Science Monthly, vol. 65, 1904, pp. 530–531.)

Many writers have laid emphasis on direct effects of environment as causes of variation. Plants may be kept small or rendered abnormal in other respects by having too little or too much water, heat, or light, or colors may be changed if the tissues are penetrated by chemicals or dyes. To keep a plant small may be considered as a direct effect of environment, but the reduction or suppression of a character is not to be confused with the substitution of a different character. That an external condition, such as temperature or humidity, enters directly into a cotton plant to change the form, texture, or hairy covering of the leaves is not to be assumed. The plant grows in a different way after the conditions are changed and brings different characters into expression.

Indirect, adaptive changes of characters in response to changes of external conditions have more significance in heredity than direct effects, because they represent activities of the plants instead of mere limitations imposed by environment. Still greater interest attaches to the more permanent changes of characters, the definite mutations or reversions that often take place without changes of environment and persist in different environments.

Many changes of expression occur regularly during the development of each plant, in producing the specialized forms of branches, leaves, and floral organs. These changes are also much greater than any induced by differences of external conditions. From the standpoint of heredity the development of each individual plant or animal should be looked upon as a process of changing characters quite as much as the development of the species. Variation in the sense of diversity of expression of characters is as normal for the species as the developmental changes are for the individual.

Many difficulties are introduced into the study of variation by failure to recognize the facts of diversity. With uniformity accepted as the normal condition, it seems logical to begin the study of heredity by seeking for the causes of changes of characters, as so many investigators have done. The nature of the problem is altered when it is perceived that diversity is the normal condition of species and that heredity provides in advance for a wide range of expression of characters. In a practical study of heredity the first object is not to learn causes of variation, which exists everywhere in the greatest abundance, but causes of uniformity, in order to establish and maintain the expression of desirable characters and avoid the expression of undesirable characters.

NEW-PLACE EFFECTS AND ACCLIMATIZATION.

The power of external conditions to induce profound alterations in the expression of characters could hardly be shown in a more striking manner than by the behavior of the foreign types of cotton

when planted for the first time in the United States. The Kekchi type of Upland cotton, grown under native conditions in eastern Guatemala, is a small, compact, early, productive plant. Raised under Texas conditions it would not have been recognized as the same species of cotton if the origin of the seed had not been definitely known. The experiment was repeated many times with different stocks of imported seed. Many other varieties from Central America and Mexico have showed similar changes of behavior on being brought to the United States.

It is no exaggeration to say that the expression of all of the characters of the Kekchi cotton is changed under the new conditions.

FIG. 1.—Leaf of unacclimatized plant of Kekchi cotton. (Natural size.)

Instead of producing a low, early, dwarf type of plant, as in Guatemala, the Kekchi cotton grows in Texas into a large leafy bush. Many of these huge, overgrown plants remain completely sterile throughout the season, but some of them produce a few small bolls. The changes in the shape and habits of the plants result from the fact that the fruiting branches of the normal plants are more or less completely replaced by vegetative branches.

In addition to these alterations in the habits of growth there are many changes in the form and texture of the leaves, the structure of the involucre, the number of carpels, and the length and abundance of the lint.

The leaves become larger, softer, and more hairy, with more numerous lobes, and have a closed sinus at the base. The extent of these changes may be judged by comparing figures 1 and 2, which represent leaves of the usual form on plants of Kekchi cotton before and after acclimatization. Both plants were grown under the same conditions at Bard, Cal., in the season of 1910. The involucres have more numerous and larger bractlets. The bolls, if any are produced, are much smaller than in Guatemala and have only three or four locks, very seldom five. The lint shortens from nearly an inch and a quarter to an inch or less and becomes very sparse. The fuzzy covering of the seeds may become abnormally developed or may show a greenish color.

FIG. 2.—Leaf of acclimatized plant of Kekchi cotton. (Natural size.)

These changes are not permanent. They represent merely a temporary suppression of the normal characters, not a loss from transmission. In five or six generations the expression of the normal characters is reestablished, and the Kekchi cotton returns to its original condition of fertility. At the same time the bolls increase in size and the fiber shows a length and abundance equal to that of the best plants of the original Guatemalan stock. The 3-locked bolls that occur frequently on the large, infertile, unacclimatized plants are replaced by a normal proportion of 5-locked bolls.

Attention was first called to this difference in the number of locks by Mr. Rowland M. Meade, at San Antonio, Tex., in the season of

1908. Most of the plants grown from imported seed were completely sterile and the others bore only a few bolls. Of 41 plants with bolls, only 5 individuals produced any with 5 locks. In adjacent rows of partially acclimatized Kekchi cotton none of the plants were completely sterile, and the proportions of 5-locked bolls were much higher, as Table I will show.

TABLE I.—*Census of the bolls and locks of unacclimatized and partly acclimatized plants of Kekchi cotton at San Antonio, Tex., Sept. 12, 1908.*

Seasons.	Number of plants.	3-locked bolls.	4-locked bolls.	5-locked bolls.	Total number of bolls.	Average number of bolls.	Percentage of 5-locked bolls.
First	41	39	202	6	247	6	2.4
Third	12	9	215	30	254	21	11.8
Fourth	7	5	81	91	177	25	51.0

Similar results were obtained in the season of 1909 at Falfurrias, Tex., where adjacent first and second season plantings of the Kekchi cotton were compared, as shown in Table II.

TABLE II.—*Census of the carpels of bolls and late buds of 25 plants of first and second year rows of Kekchi cotton at Falfurrias, Tex., in 1909.*

Plant No.	First-year planting (from imported seed).						Second-year planting (from seed grown in Texas).					
	Bolls.			Buds.			Bolls.			Buds.		
	3-locked.	4-locked.	5-locked.	3-locked.	4-locked.	5-locked.	3-locked.	4-locked.	5-locked.	3-locked.	4-locked.	5-locked.
1										22	67	1
2				2	26	4		4			38	2
3				1						3	78	8
4										11	15	
5		1			2					2	68	1
6				3	3							
7				2	20					10	38	
8		6		1	5					4	43	3
9	2	8		9	9					4	69	
10				3	7			8	1	3	69	4
11										2	9	
12		5		4	24					2	1	
13	2	5		20	17			1			7	
14				4	1						1	
15										2	17	1
16		1			18		1	1				
17					1						4	
18					3					1	24	
19										5	50	6
20				7	21					9	47	2
21				11	10					8	51	6
22		2		4	39	2				4	30	2
23				3	8							
24				3	4		1			3	25	1
25	2	2		2				15		5	39	1
Total	6	30	0	79	218	6	2	29	1	100	790	38
Percentage	17	83	0	25.9	71.7	2.3	6.3	90.1	3.1	10.8	85.2	4.1

A more definite indication of the superior fertility of the second-year planting was afforded by the presence of numerous individuals that produced more numerous and larger bolls than any of the first-

year plants. A count of the bolls of 10 such plants showed a total of 210, of which 2 were 3-locked, 190 4-locked, and 18 5-locked. The 10 fertile plants had less than 1 per cent of 3-locked bolls and 8.5 per cent of 5-locked bolls.

Other examples of variation in the proportion of 5-locked bolls were afforded by a series of plantings of acclimatized and unacclimatized Kekchi cotton in adjacent rows in several localities in California in the season of 1910. Localities with warmer climates produced lower percentages of 5-locked bolls, though the season of planting and the nature of the soil evidently affected the result in ways that other experiments have shown to be possible. Drought or other adverse conditions that reduce the crop also diminish the proportion of 5-locked bolls. In the hot interior valleys of California the proportion of 5-locked bolls in the unacclimatized stock fell nearly as low as in Texas. But in the acclimatized stock the proportion of 5-locked bolls often ran higher than in Texas. (See Table III.)

TABLE III.—*Census of bolls and locks of unacclimatized and acclimatized Kekchi cotton in 10 plantings in California (season of 1910).*

Localities.	Unacclimatized stock (from imported seed).					Acclimatized stock (raised for five seasons in Texas).				
	Number of plants.	3-locked bolls.	4-locked bolls.	5-locked bolls.	Percentage of 5-locked.	Number of plants.	3-locked bolls.	4-locked bolls.	5-locked bolls.	Percentage of 5-locked.
Red Bluff	19	3	137	34	19.5	20	3	322	256	44.1
Chico	20	6	304	43	12.2	23	4	175	275	60.6
Stockton	7	0	125	67	34.9	14	0	71	200	73.8
Visalia	25	16	325	115	25.2	3	0	8	7	46.6
Stockdale	17	3	150	105	40.7	19	0	96	[1] 444	82.2
Semitropic	16	61	451	21	3.9	16	2	96	377	79.4
Glendale	20	10	284	145	33.0	20	2	128	347	72.7
El Centro	19	40	77	4	3.3	......	......	......	......	......
Meloland	18	13	44	0	.0	20	5	219	121	35.1
Bard	20	181	523	23	3.2	10	7	653	730	52.5

[1] In this instance two 6-locked bolls were included with the 5-locked.

In hot climates, as in southern Texas and in the interior valley of California, adjacent rows planted with acclimatized and unacclimatized seed of the Kekchi cotton show striking contrasts in vegetative development and fertility. The unacclimatized plants grow to several times the size of the others and produce scarcely any cotton, while the acclimatized plants remain small and bear good crops (Pl. I, fig. 1). In the cool climate of Glendale, Cal., near the coast, the rows appeared much more alike (Pl. I, fig. 2), though the acclimatized stock had somewhat larger bolls and better lint, as though a simple selection had been used. The Kekchi cotton also behaves in a nearly normal manner in Kansas and in Maryland.

In acclimatizing a superior type of cotton we do not make the variety over by creating new characters, but merely bring back to

normal expression characters that the variety is already known to possess. Success with this kind of acclimatization depends primarily on knowledge of the normal habits and characters, so that the variety may be guided back to normal behavior by the selection of the individuals and progenies that show most definite and regular expression of the normal characters.

As the variations induced by the new environments seem to extend quite outside the range of ordinary accommodations to external conditions, they have been described under a special name, "new-place effects." The acclimatization of such plants as cotton might be described as a process of avoiding or eliminating new-place effects. Though the new types of cotton have been brought from tropical countries, high temperatures seem to be the chief cause of abnormal behavior in the United States. The summer climate of the Southwestern States is much hotter than that of many tropical countries. Acclimatization might be said in this case to result in greater resistance to heat, for the processes of growth are no longer affected by the high temperatures that induce abncrmal development in plants raised from newly imported seed.

PERSISTENT TRANSMISSION OF LATENT CHARACTERS.

The transmission of latent characters, though familiar to Darwin and many other investigators, is still treated by many writers as a special condition, as in Mendelian hybrids. In reality the latent or variable characters of a species are vastly more numerous than the characters that are expressed with regularity. Instead of being considered rare or exceptional, latency should be recognized as a universal, underlying fact of heredity. Taxonomists prefer to consider only the constant characters, those that are shown by all the members of the species, but the variable characters are significant in heredity and breeding. The same series of variations may run parallel through whole series of related species and genera without becoming established as uniform, taxonomic characters in any of them. Though there seem to be no limits to the transmission of ancestral variations, expression remains limited in each case to the relatively small set of characters that can be shown in a single individual.[1]

[1] Though the formal distinction between transmission and expression seems not to have been drawn, many passages in the writings of Galton present contrasts between latent and patent characters, like the following example:

"From the well-known circumstance that an individual may transmit to his descendants ancestral qualities which he does not himself possess, we are assured that they could not have been altogether destroyed in him, but must have maintained their existence in a latent form. Therefore each individual may properly be conceived as consisting of two parts, one of which is latent and only known to us by its effects on his posterity, while the other is patent and constitutes the person manifest to our senses." (See Galton, Francis, "On Blood-Relationship," Proceedings, Royal Society of London, vol. 20, 1872, p. 394.)

The content or sum total of transmission is increased when new characters are added in the constructive evolutionary progress of a species, but there is no reason to assume that characters once developed ever cease to be transmitted. Evolutionary progress often involves the suppression of some of the more primitive characters, but the substratum of transmission remains; the pandoric equipment of the germ cells is not diminished. The development of each generation follows the path of all the preceding generations. The facts of reversion and recapitulation show that latent and rudimentary characters continue to be transmitted for hundreds and thousands of generations after normal expression has ceased. Socrates described the soul of man as "something sturdy and strong, imperishable by accident or wear," and so it may be said of transmitted characters, that they seem to have a permanent existence, preserved and passed down through unbroken lines of progency.

The persistent transmission of latent characters becomes all the more significant as an indication of the nature of heredity when it is considered that the suppression or reduced expression of characters is a very important factor of evolutionary progress. The addition of any new organ or function is likely to involve reductions or suppressions of other organs and functions, like the progressive reduction of teeth and other bones of the head in the more advanced, large-brained races of mankind. Viewed merely from the standpoint of characters as independent units such reduction may be confused with degeneration, but not when viewed from the standpoint of the species. An abnormal return of a reduced character to full expression is considered as a mark of degeneration, like the heavy jaws that are supposed to characterize certain classes of criminals.

The idea that the characters of adult organisms are represented by discrete particles or "units" in the protoplasm was developed by Darwin in the theory of pangenesis and elaborated by Weismann in his doctrine of the continuity of the germ plasm. In order to explain the inheritance of characters supposed to be acquired from the external environment, Darwin assumed that units or pangens representing the characters migrated into the germ-cells from the various parts of the body. Weismann denied the reality of such supposed acquirements of characters from the environment, holding that the germ plasm is not affected by the vicissitudes of the parent organism.

The persistence of latent characters in transmission shows that the germ plasm carries not only the characters that are to be shown by the organism, but also the differences that are to appear among its descendants. In other words, continuity of transmission provides for variation, or discontinuity in expression. In view of the fact that nothing is known regarding the nature of transmission, there is no way to determine whether the characters are really represented

by separate entities in the germ cells. The relations that govern the expression of the characters are of more immediate importance in the study of heredity.

The practical value of selective breeding as a means of regulating the expression of characters is quite independent of the idea that selection affects the transmission of characters. The influence of external conditions upon expression can also be recognized without supposing that new characters have been introduced into transmission. The influence of external conditions is not limited to the usual adaptive changes or accommodations, but sometimes serves to recall remote ancestral characters to expression. The new-place effects exhibited by the cotton plant may be considered as examples of reversions induced by changes of external conditions. The more extreme cases of new-place effects might be described as wholesale reversions to ancestral characters, all of the normal characters being suppressed.

REAPPEARANCE OF SUPPRESSED CHARACTERS.

The nature of the variations that continue to appear in selected strains can not be understood or the causes of such variations appreciated without taking into account the reserve stock of latent ancestral characters that can be recalled into expression. Selection serves to keep undesirable characters out of expression, but it does not put an end to the transmission of such characters or prevent their return to expression in later generations.

The rule that like parents produce like offspring represents only one phase or condition of heredity, partially attained after normal diversity has been suppressed by selection or line breeding. The production of like from like is the aim of the breeder, though he frequently finds that like produces unlike. The wider rule of nature is that unlike parents produce unlike offspring, not only through resemblance to the two parents, but through atavism, or reversion to more remote ancestors. Normal heredity should be considered as a group phenomenon. The diversities shown by ancestors and relatives are to be taken into account as well as the characters of select individuals or pure lines, if the full range of variation is to be learned.[1]

Without knowing the range of diversity of the natural group the full possibilities of improvement of a domesticated plant can not be

---

[1] This idea has been stated very clearly by Davenport in the following paragraph:

"To define 'heredity' as the direct and personal relation between the individual parent and the individual offspring is not only to restrict its meaning within too narrow limits but to destroy its significance to the breeder and deceive him as to the actual facts of transmission during descent. 'Heredity' properly refers to the group that constitutes the parentage and the related group that constitutes the offspring." (See Davenport, E., "Principles of Breeding," p. 473.)

judged. Extensions of agriculture into new regions and applications of plant products to new uses are continually calling for improvements along new lines. Characters previously disregarded in selection may become of primary importance and lend a corresponding interest to the varieties or species that are found to meet the new standard of desirability.

Valuable indications for further improvements of types already in use are often to be gained from the variations of related species, and especially from those that have not been reduced to uniformity by selection. Thus a recognition of the existence of weevil-resisting adaptations in stocks of Upland cotton cultivated by primitive Indian tribes in Guatemala and Mexico has opened the way to a study of weevil-resistant characters and cultural factors in the Upland varieties of the United States. After the more definite specializations of the Central American types of Upland cotton were known it was possible to recognize and appreciate the value of parallel series of variations that occur in our United States Upland varieties, though not previously recognized.[1]

That each of the lines of descent of a natural species can transmit the endless peculiarities of its highly diversified ancestry may be difficult to believe until the nature of the process of transmission can be understood, just as it is difficult for the average person to credit the idea of sending many simultaneous messages over the same wire. The only alternative to the acceptance of multiple transmission and variable expression is the assumption that all the mutative variations arising in selected stocks represent the reorigination of the diverse characteristics that the selection of pure lines is supposed to eliminate.

Though many of the facts of biology can be stated in physical terms, the best analogies of heredity are psychical rather than physical. Psychologists have long recognized the probability that the mind retains a permanent record of all the multitudes of impressions received from the senses. The retention of large numbers of impressions in the mind may be compared to the process of transmission, while the return of the different groups of impressions to consciousness is like the expression of characters in individual organisms. Though only a few of the impressions are capable of voluntary recall by the conscious memory, the subconscious record endures and is often revealed in unexpected flashes, analogous to the occasional return of remote ancestral characters to expression. To describe heredity as organic memory is not a mere figure of speech, for the mental faculties are a product of heredity, no less than the physical body.[2]

---

[1] Weevil-Resisting Adaptations of the Cotton Plant. Bulletin 88, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1906.

[2] Cook, O. F. Heredity Related to Memory and Instinct. Monist, vol. 18, no. 3, 1908, pp. 363–387.

Heredity may be considered as an organic memory of the previous paths of descent, a memory that is transmitted because it inheres in the protoplasm of the germ cells. There is the same reason for holding that characters have a physical basis or representation in the protoplasm of germ cells as for supposing that impressions have a physical basis in the brain cells. That the mind is able to receive, retain, associate, and reproduce impressions and ideas is a fact even more familiar to us than heredity, yet of memory as a mechanical process we have as little conception as of heredity.

Neither of the logical alternatives so much discussed by the earlier investigators affords an adequate statement of the facts of heredity. There is as little advantage in assuming a definite preformation of each generation in the germ cells of the parents as in holding that reproduction involves an entirely new formation or epigenesis. If taken in sufficiently general senses, both doctrines are true. The forms of the ancestral generations are carried over to their descendants and yet each individual is formed anew after its own unique pattern.

The members of a species appear alike if compared with another species, but when compared more closely with each other they are found to be different. Such diversity is not a mere failure to hit the center of the target of ideal uniformity, but is a positive essential fact that must be taken into account in understanding the nature of heredity. The normal mechanism of heredity that maintains the existence of a species is not adjusted to produce a mere succession of identical individuals.

Though all the members of a species follow the same general course of development, they do not trace exactly the same courses. The fact of evolutionary progress shows that there is no absolute limitation to ancestral characters or combinations. The pathway of hereditary development in a natural species should not be thought of as a simple, narrow line, but as a broad track with many interlacing paths followed by different individuals. The individual differences are to be recognized, as well as the more distinct and widely separate alternatives of expression manifested in sexual specializations and other definite forms of diversity. In species that are divided into sexes or castes, two or more separate courses of development may be recognized. There are many different degrees of such specializations, as of other characters.

Instead of assuming in advance that heredity represents either preformation or epigenesis it is better to begin by recognizing that the course of development is not definitely fixed either before or after conjugation takes place. Many changes and alternatives of expression are possible. Each individual is different, though each is a part of the same network of descent. It is this conception of

hereditary development as the following of a broad, well-beaten track or netlike pathway of development that should be substituted for the older assumptions. The controversies of biologists over preformation and epigenesis are closely analogous to those of anthropologists over monogenesis and polygenesis, the question whether mankind had a single or a multiple origin. Confusion arises in both cases from the failure to perceive the same fact—that evolutionary progress toward new characters is not a matter of single variations or of simple lines of descent, but is a change in a broad network of descent. In applying this distinction in anthropology the term "eurygenesis" was suggested as an alternative of monogenesis and polygenesis. Primitive men, like their present representatives, may be supposed to have constituted a large diverse group rather than a small uniform group or a series of entirely independent groups.[1]

If the mechanical conception of heredity as something in the nature of a system of invisible models, patterns, or determinant particles is to be retained, it must be vastly expanded to include all the different variations or alternatives of expression that are found among the members of normally diverse, freely interbreeding species. Other methods of reproduction, by restricted descent, enable the manifestations of heredity to be narrowed down to conditions of uniformity and definitely contrasted characters which can be interpreted by a simple theory of alternative transmission of character units, but to give exclusive consideration to these specialized states of uniformity is not to solve the underlying problem of normal diverse heredity, but rather to avoid it. It is much easier, of course, to trace the behavior of aberrant characters or lines of descent, those that wander away from the pathway of normal development or are artificially separated from it. This explains why so much more attention has been given to uniform line-bred groups than to diverse groups interbreeding in a normal network of descent.

The problem of heredity is not merely to provide for the formation of the small number of external differences commonly referred to as characters, but for the formation, specialization, and coordination of the almost infinite number and variety of cells that compose the tissues and organs of the bodies of plants and animals. And when it is remembered that each cell must be supposed to bear the determinants for reproducing all the other cells, the mechanical theory becomes a maze of inconceivable complexity. It is true that most of the cells of the higher animals are so specialized that they no longer serve purposes of reproduction, but with plants a large proportion of the cells retain the power of producing all the other kinds of cells. Cases where the leaves as well as the stems are able to produce new individuals by budding have been looked upon as examples of

[1] Cook, O. F. Kinetic Evolution in Man. Science, n. s., vol. 15, June 13, 1902, p. 927.

reproductive specialization, but should be considered rather as representing incomplete vegetative specialization.[1]

The germ cells must be supposed to carry the determinants, not merely of a few general, external features, but of all the internal organs and of the multitudes of cells that are to compose the bodies of their varied posterity. Every external character of a plant like cotton is a collective result of coordinated activities of vast numbers of cell individuals, each highly complex in itself. There is no more need of specialized determinants for the distinctive features of a variety than for the features that are not peculiar to the variety.[2]

It may be that the predication of determinant character units brings biology into more logical accord with corpuscular theories of physics, but this is not so important as to have biological theories accord with biological facts. Only a few of the characters of plants and animals appear to have definite reactions like those that physical chemists explain by their theories regarding the structure of molecules.

To compare organisms with crystals is a very inadequate analogy, but it is at least better than the analogy of amorphous compounds. Because the crystals of a certain substance are always of the same general form it is not held that they are controlled by special particles or determinants. To say that the substance has a property of crystallization does not explain how the crystals are formed, but it at least avoids the need of making a more complex and improbable assumption that there are special particles to control the different angles and planes of crystallization. The same substance may crystallize in a different system when placed under different conditions, but this does not compel us to suppose that new characters have been added. There are regular systems of leaf arrangement in plants even more complicated mathematically than the systems of crystallization in chemicals, but phyllotaxy is subject to variation like other characters of plants.

---

[1] In addition to the usually cited illustrations of this condition in Bryophyllum and Begonia, another example was noted by Hance in 1849 in a Chinese plant, *Chirita sinensis*, of the family Gesneraceæ. In this case, as in Begonia, the young plants "sprang indiscriminately from the costa, primary veins, and connecting parenchyma." Hance also refers to reports of the same phenomenon in Ornithogalum and Drosera, members of two other widely separated families. (See Hance, H. F., "On Some Chinese Plants," Hooker's Journal of Botany and Kew Garden Miscellany, vol. 1, p. 141, pl. 5, fig. c.)

[2] That the Mendelian theory of alternative inheritance may not apply to the more fundamental characters has been recognized in the following passage:

"Aside from these cases which show a distinctly non-Mendelian mode of inheritance, it must be remembered that Mendelian analysis can be made only in the presence of differential unit characters possessed by individuals capable of life and of sexual reproduction, and that therefore there can be no test, except under rare circumstances, of the Mendelian nature of the more fundamental vital characters. This leaves it an open question whether the whole of the germ plasm is a complex of such genes as those which give rise to the phenomena of unit characters, or whether, with its wonderful general powers of assimilation, growth, and reproduction, it consists of a great nucleus of which the genes are relatively superficial structural characteristics." (See Shull, G. H., "Germinal Analysis through Hybridization," American Philosophical Society, vol. 49, 1910, p. 290.)

Regularity of expression, whether of frequency or of degree, affords no reasons, either logical or biological, for supposing that the characters of organisms are determined by preformed models or by discrete particles representing different characters. The doctrine of determinants could be applied with more reason to the expression of characters than to transmission. External conditions and internal secretions are already known to act as determinants of expression. That germ cells might be charged in advance with such determinants of expression is quite conceivable, and this supposition would accommodate all the facts that have been used to support the theory of alternative transmission. A convenient division of labor might be arranged on this basis, the undifferentiated protoplasm being considered as the seat of transmission of all the characters, and the chromosomes as determinants of expression, with specialized chromosomes to represent the definitely alternative characters.

FACTORS THAT CONTROL EXPRESSION RELATIONS.

Whatever the future may bring in the way of discoveries regarding the nature of transmission and expression, it is desirable to avoid further confusion of the two processes. Variations of plants or animals of the same species recently descended from common ancestors represent differences in the expression of the characters rather than differences of transmission.

The processes of expression evidently do not operate independently for each character, but have mutual interrelations, often very complex. The expression of one character may depend upon or conflict with the expression of other characters. In order to secure and maintain the highest degree of expression of desirable characters it is necessary to understand their expression relations. Unless these relations are taken into account the breeder may waste his time in vain attempts to establish the expression of incongruous and unstable combinations of characters. The study of heredity, as far as it is concerned with actual variations of plants and animals, is the study of expression relations. The control of expression relations is the art of breeding.

Potency is the name applied to inherited tendencies of expression. It is not sufficient to define potency as the power of transmitting characters, for the power of simple transmission of characters is a general property of organisms. Potency involves not merely the transmission of a character, but also the inheritance of a condition or factor of expression, something that brings about a strong and regular expression of the character in each generation instead of a weak, irregular, or intermittent expression.

50600°—Bull. 256—13——3

Something more is required for expression than for transmission alone. There must be favorable conditions, internal and external, for each particular character, if full expression is to be gained. Though the mechanism of expression, like the mechanism of transmission, is still unknown, it is evident that external conditions, methods of breeding, and relations with other characters are factors that affect the mechanism of expression, though having no corresponding influence over the mechanism of transmission.

Though some changes of expression relations evidently arise inside the germ cell, others are induced by external conditions. It is safer, for scientific progress, to begin by considering the changes that can be influenced by external conditions or by breeding, and to use these as a basis for understanding the internal relations and the nature of the mechanism of expression. To proceed otherwise, by drawing out series of logical deductions regarding processes that are not open to direct observation, is to disregard the possibility of securing more practical points of view.

Even if it could be shown that certain characters have their residence in certain particles of the protoplasm the problem of controlling the expression of the characters would remain. In all probability it would still be necessary to deal with the characters through the external methods of influencing expression, rather than by manipulating the determinant particles inside the germ cell.

The most effective methods of selection are those that take into account the potencies of the characters. Instead of selection being based merely on the degree of expression attained in the individual parent, it should be based on regularity of expression in the progeny, as is most definitely recognized in the centgener methods applied by Hays to the breeding of wheat. A higher degree of expression may be attained in a few individuals or may result from some unusually favorable external condition, but without establishing a definite potency in the stock. Selection of the lines of descent having the largest and most stable expression of a desired character serves to establish and stabilize such expression, though mutative reversions and degenerate individuals continue to appear.

The effect of selection to increase the yield of a crop is explained by the greater uniformity secured by the rejection of inferior individuals. Yet selection alone can not be relied upon to maintain the largest possible yields. This has been demonstrated in many cases where conjugate hybrids of two strains have been found to produce much larger and better crops than either of the parent varieties grown under the same conditions. Increased vigor secured by crossing has the same practical advantage in improving the crop as planting in a richer soil or using more fertilizer. The superior vigor and

fertility of the hybrids depend largely on their greater powers of resistance to unfavorable conditions.

CORRELATION AND COHERENCE IN EXPRESSION.

The value of correlation as a guide to selection has been recognized, and attempts have been made to discover useful correlations by elaborate systems of measurements. Regard for the distinction between expression and transmission makes it possible to place the study of correlation on a broader biological basis. Many so-called correlations, such as correlations between size and weight or between length of internodes and total height of plant, represent merely different mathematical statements of the same fact and have very little biological significance.

Biological correlations are to be interpreted in the light of the general fact of coherence of characters in hybrids, the tendency of characters derived from the same ancestral group to remain associated in expression. Characters that remain coherent in hybrids between different species are likely to be correlated in variations of unhybridized stocks. In other words, phylogeny may explain coherence and correlation.

Lack of coherence allows free combinations between the characters of the two parents, according to the laws of chance. This represents the typical form of heredity from the standpoint of the Mendelian theory, but other relations seem to be more common and more important in breeding. The expression relations of the characters in wild or unimproved allies of domesticated species often afford the best clues for the solution of breeding problems that depend upon coherence or correlation.

One of the limitations of the Mendelian theory of heredity is that it is based so largely on the idea of pairs of contrasted characters supposed to be separately transmitted, as in sexual differences. In less specialized kinds of characters, expression has not merely two alternatives, but many possible variations or degrees of expression. Only a few characters have the definitely contrasted polarity of expression of the typical cases of Mendelism. Even among characters that segregate in the later generations in a definite Mendelian manner only a few show either of the parental alternatives of expression in the first or conjugate generation of hybrids. In the great majority of cases the first generation shows different degrees of blended or graded intermediate expressions of the parental characters, or even characters that did not appear in the parents. Thus, when a variety of cotton with naked seeds is crossed with a variety having white fuzz on the seeds the hybrids are likely to have green fuzzy seeds.[1]

[1] Cook, O. F. Reappearance of a Primitive Character in Cotton Hybrids. Circular 18, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1908.

All the facts of Mendelism seem to accord quite as well with the idea of alternative expression as with that of alternative transmission. The more careful investigators of Mendelism are beginning to recognize that only a relative "purity of germ cells," instead of an absolute purity, can be claimed. Occasional variations are found even in characters that have shown the typical Mendelian behavior in large numbers of cases.

Interesting examples of reversion and variable expression of the starch character in sweet corn have been reported recently by East and Hayes. Two explanations are suggested, either that the hypothetical character units, or "genes," are broken up into fractions, some of which remain in the recessive strains, or that the starchy character has reappeared as a result of new variation. The idea of frequent origination of the same character receives more favorable consideration, as the following statement will show:

> Either homozygous recessives (and likewise dominants) are not complete segregates, but products of a partial quantitative separation of genes allowing traces of the dominant character to remain, traces which may sometimes accumulate sufficiently to bring out the dominant character; or, progressive variations are constantly taking place in small numbers, most often along paths that have been passed before.
>
> It is our opinion that dominant starchiness—if it is the same dominant starchiness—has been formed anew. It occurs too rarely to support a partial segregation theory, such as Morgan's. If it is asked why starchiness is the character that arises anew rather than another variation, it is suggested that the peculiar chemical structure of the germ cell of maize may be such that a molecular readjustment is much more likely to bring about starchiness than any other variation. Such a path of least resistance for variations might account for the many cases in animals and plants where the same variation has apparently occurred again and again.[1]

With latency and alternative expression of characters recognized as general conditions of heredity, it becomes unnecessary to resort to theories of alternative transmission, incomplete segregation, or frequent reorigination of characters. If the character units can be broken up into fractions and transmitted in different quantities or regenerated after having been removed completely from the stock, their nature must be very different from what was formerly assumed in the theory of pure germ cells. Such modifications amount to a practical abandonment of the definite features that have hitherto served to recommend the idea of alternative transmission. If each of the starchy variations of sweet corn is to be considered as an origination of a new character, the same reasoning should be applicable to any other character, such as color blindiness, that does not appear in the immediate parents.

[1] East, E. M., and Hayes, H. K. Inheritance in Maize. Bulletin 167, Connecticut Agricultural Experiment Station, 1911, pp. 42–43.

Greater permanence can be ascribed to the underlying mechanism of heredity when the distinction between transmission and expression is recognized, and there is less need of insisting upon discrete units to represent the different characters. Whatever the nature of the mechanism that transmits the characters, it need not be supposed to change because the factors of expression are altered. Many different fabrics can be woven on the same loom by merely changing the patterns. The differences shown in the same stock of plants or animals represent different patterns of expression, all based on the same equipment of transmitted characters.

Even in cases where sex has been found to be determined in advance by the presence or absence of an accessory chromosome in one of the parent germ cells, it is hardly to be held that the sexual characters themselves are directly represented by this chromosome any more than by the heat, sunlight, or other external conditions and internal secretions that have been found to influence the expression of sexual characters in other cases. Increase in the proportion of males in hybrid stocks over the proportions shown in the parent varieties also indicates that the determination of sex depends upon other factors than simple alternative transmission of the sexual characters.[1]

The fact that males are produced from unfertilized eggs of bees and other hymenopterous insects does not warrant the inference drawn by some writers that the female characters are not transmitted by the female sex. Indeed, it is now known that female insects as well as male sometimes develop from unfertilized eggs. Sexual differences, like contrasted Mendelian characters, may be looked upon as examples of alternative expression instead of alternative transmission. Peculiarities of one sex are transmitted by the opposite sex as well as by the same sex and may even be brought to expression, as in an abnormal hen that grows long tail feathers and crows, or in a caponized male that hovers chickens. The specialization of sexual characters has gone on independently in so many different groups of plants and animals that the same relations of expression are not to be expected in all cases. To generalize on sexuality as a Mendelian character is to substitute the same abstract term for a widely varied series of biological facts.

Dimorphic forms of leaves and branches in plants are analogous to the sexes and castes of animals. Each plant may be considered as a colony composed of several different kinds of internode individuals, often capable of an independent existence. The different kinds of internodes show alternative or contrasted expression of characters, like Mendelian or sexual differences. After several of the

[1] King, H. B. The Sex Ratio in Hybrid Rats. Biological Bulletin, vol. 21, July, 1911, p. 104.

lower internodes of a cotton plant have produced vegetative branches there is an abrupt change to a different type of branches, those that bear the flowers and fruit. There can be no question that dimorphic differences represent changes of expression rather than changes of transmission, for the contrasted characters are shown among the internode members of the same plant.

In addition to the functional difference the fruiting branches of the cotton plant have other specializations, like the secondary sexual characters of animals. The leaves of the fruiting branches are usually somewhat different from those of the vegetative branches, and in Egyptian cotton the stipules of the two kinds of branches are quite distinct. The shortening of the internodes of the fruiting branches, as in the so-called "cluster" varieties of cotton, does not extend to the vegetative branches. Varieties of cotton that do not maintain the normal specializations of the different kinds of branches, leaves, and floral parts are undesirable. Abnormal fruiting branches usually produce abnormal leaves and involucres and frequently abort the buds or the bolls.

That the expression of one character often involves the suppression of another is true in the development of a race as well as in the growth of an individual, though it does not appear that the suppressed characters are excluded from transmission. Abrupt changes or contrasts of expression are evidently as natural as gradual changes and as little in need of being explained by theories of alternative transmission.

In the Mendelian system, the suppression of a character to a condition of latency has to be explained by the presence of another inhibiting unit. As Castle has recently shown, it is possible to make very complicated Mendelian problems out of facts that are capable of simple physiological explanations.[1]

THREE KINDS OF EXPRESSION RELATIONS.

In order to facilitate a more definite study and description of the relations of expression and to avoid the confusion introduced by theories of variable transmission, three principal types of such relations may be recognized. When the expression of one character

[1] "Consider how one unproved hypothesis has been added to another. First, it is assumed that in hornless animals a gene for horns has either been lost or is inhibited. It is equally probable that no gene has been lost and that nothing is inhibited. Secondly, it is assumed that one inhibitor is inferior to one horn-gene in power, but that two inhibitors surpass one horn-gene, yet two inhibitors are themselves overpowered by two horn-genes; without all three of these ungrounded assumptions of the relative valency of imaginary genes the explanation fails altogether. Further, it is assumed that the female is capable of carrying two inhibitors, but the male only one. And, finally, when this colossal structure of hypothesis encounters one well-known physiological fact, the result of castration, that fact is calmly brushed aside. Is this a desirable extension of Mendelian interpretation?" (See Castle, W. E., "Are Horns in Sheep a Sex-Limited Character?" Science, n. s., vol. 35, Apr. 12, 1912, p. 575.)

depends upon or conduces to the expression of another character the relation may be called "symphanic." When the expression of one character inhibits or interferes with the expression of another the relation may be called "antiphanic." When the expression of one character neither favors nor interferes with the expression of another the relation may be called "paraphanic."

These terms can also be defined from the standpoint of correlation, though including a wider range of phenomena than are usually considered in statistical studies. Characters may be called symphanic when they show mutual or positive correlations of expression, antiphanic when they show negative or antagonistic correlations, and paraphanic when there is an absence of correlation.

It may be objected that more words are unnecessary, since the facts can be stated in terms of correlation. As long as the facts are viewed only from a mathematical standpoint the terminology of correlation may be sufficient, though it is often inadequate if not actually misleading, for biological statement of the facts. Negative correlation (antiphany) and absence of correlation (paraphany) are no less positive facts from the biological standpoint than the cases that are described as positive correlation (symphany). It may be that the meaning of the term "correlation" will become modified in practice so as to have more of a biological and less of a mathematical significance. The object to be gained in the meantime is the recognition of the practical importance of the study of expression relations from the biological standpoint, instead of depending upon the mathematical method of the empirical discovery of such relations.

Some writers have concluded that correlations are too rare to be of use in practical breeding, because of the many cases of apparent absence of correlation that result when measurements are applied at random, in attempting to make empirical discoveries of correlations. While it is probably true that the paraphanic characters outnumber the symphanic and antiphanic characters, it has also to be considered that many of the so-called characters employed in the search for correlations represent merely formal statements, framed without regard to the real relations of expression.

With characters framed from the biological standpoint it is to be expected that the laws of correlation, of variation, and of coherence of characters in hybrids will be found to have very general application, as long since recognized by one of the greatest of botanical naturalists.

> In all stable groups, whether of higher or lower rank, there should be some correlation of structure in every organ, which it is the systematist's part to trace out and rate at its true value.[1]

[1] Spruce, R. Equatorial-American Palms. Journal, Linnean Society, Botany, vol. 11, 1871, p. 91.

MEASUREMENT OF EXPRESSION RELATIONS.

It is often interesting, and may sometimes be important, to make accurate determinations of the extent of correlation in the expression of two characters in a particular group of plants or animals. Elaborate systems for measuring and expressing different degrees of correlation have been recommended by mathematical biologists. If these relations of expression represented natural constants like the atomic weights of elementary substances or the angles of crystals, the labor of very accurate determination of all such relations might be justified. But there is no reason to believe that relations of expression are less varied than other biological phenomena. They are often changed in the same group or even in the same individual under different conditions of existence. Correlations will appear constant, of course, as long as the expression of the characters is not changed, but any influence able to disturb expression is likely to interfere with correlation as well.

It is manifestly desirable that biological study of expression relations precede mathematical study to avoid the waste of labor in ultra-accurate determinations of relations that have little or no biological significance. An almost infinite number of mathematical relations can be formulated among the parts of any of the higher plants or animals. If the measurements of all conceivable relations were considered necessary as a basis of biological study the future of biological science might well be considered hopeless. It is a mistake to consider the making of statistical measurements as an independent method of biological investigation. The importance of biological statistics resides almost entirely in their value as a more direct and accurate method of stating relations revealed or suggested by familiarity with facts gained through other methods of investigation.

When mathematical analysis precedes biological analysis the facts are likely to be brought into entirely artificial and misleading relations. A fact that appears altogether trivial from the statistical standpoint may be extremely significant from the biological standpoint, such as the appearance of a few individual mutations among thousands of unvaried examples of a pure stock. The most striking example of correlation, where groups of characters derived from the same parent show coherence in expression, are capable of direct observation, without the need of mathematical demonstration. Mathematical statements of such compound relations are difficult to frame, and the facts are not rendered any more intelligible or more practically useful after such treatment. In critical cases it might be important to learn which of a series of coherent characters were more closely associated, but this would require only a comparison of simple correlations. There would still be no practical need of reducing a compound correlation to a mathematical expression.

The idea that all biological facts are enhanced in value or interest by being stated in mathematical form is to be understood as one of the results of the undue emphasis generally placed on mathematical studies in educational institutions. It is easier to occupy the student with mathematical formulæ than to develop his interest in the multitudinous details of plant or animal life, and allow him to secure the familiarity with nature that is necessary as a basis of biological judgment. The tendency of educational institutions is to formal instruction in biology, as in other subjects. The mathematical substitutes for biology afford more satisfactory materials for pedagogic purposes, and especially for dealing with large bodies of students.

Coefficients of correlation between different characters, such as stature and susceptibility to disease, are useful, of course, for insurance companies interested in the longevity of mixed populations, but nobody has explained how such coefficients are to be used by the breeder of select strains. Selection, with the breeder, is not a matter of taking average risks on a large number of individuals, but of finding and propagating the best individuals. Such selection must be based on biological types, not on mathematical types or statistical averages.[1]

To say that a variety or type of cotton has a tendency to variation in a certain direction may seem too loose and indefinite for scientific purposes. Writers who aim at mathematical precision often object to such statements. But when the facts themselves are indefinitely variable it is not unscientific to describe them in appropriate language. To say that a stock has a tendency to vary merely means that some individuals are likely to show the variation in question, while others do not, which is true of many characters. While it is interesting in all such cases to make more accurate determinations of the extent of variations in different stocks or in different conditions, it is first necessary to recognize that the tendency exists. To record such as observation is quite as proper and as truly scientific as for an explorer to record the general position of a range of mountains, though he may not be able to climb the peaks or even to establish their exact locations.

[1] Bateson has called attention to the fact that mathematical treatments may conceal biological differences which are apparent from direct observation: "As a matter of fact, even in the case of Nigella, differentiation was detected not by the seriations, but by common observation. When the differentiation has been once detected, its influence can be seen in the seriations. This is a mere accident. If the material had happened to contain a certain proportion of a second race with a 'mode' on 10 or 13 and a secondary 'mode' on 8—a condition familiar in plants (from F. Ludwig's beautiful researches)—the differentiation might have been completely masked in the seriations. As it is, the seriations alone contain nothing which prove the existence of differentiation. We happen to know otherwise that high numbers are associated with centrals and lower numbers with laterals. This is not revealed by the seriations. For all they show, the irregular distribution might be due to ordinary discontinuous variation, obeying the laws which F. Ludwig has shown such distributions commonly obey." (See Bateson, W., "Heredity Differentiation and Other Conceptions of Biology." Proceedings, Royal Society of London, vol. 69, p. 205.)

It is not surprising that investigators who approach biology from the standpoint of the physical sciences, without becoming familiar with the protean diversity of species in nature, should overlook the essential flexibility of the processes of reproduction. Elaborate measurements often convey misleading impressions of regularity or secure too exclusive attention to phenomena that lend themselves to mathematical forms of expression. The following statement in a recent review of biometrical literature affords further evidence that this danger is beginning to be appreciated:

> One who follows the current literature of agricultural science, in a broad sense of the term, can not fail to be struck with the rapidly increasing use of these mathematico-statistical methods during the last few years. In so far as the methods are correctly and appropriately used this is a most commendable movement. But it must always be kept in mind not to let admiration for the method per se blind one as to the real significance and importance of the biological problem attacked. The futility of dealing biometrically with data or problems which lack a sound biological basis is obvious. The indiscriminate application of biometric methods to all kinds of data is easily seen upon critical examination to have only so much value or validity as resides in the original data themselves. It is particularly important that this point be kept in mind in agricultural work along biometric lines, because of the great ease with which mere statistics can be collected in this field and the consequent temptation to collect them without critical consideration of their meaning and worth.[1]

UNIFORM EXPRESSION OF CHARACTERS.

Uniform expression of characters is secured in domesticated varieties by vegetative propagation or by selective line breeding. It is not a typical condition of heredity in normal species nor an ideal in eugenics. Agricultural breeding is largely a problem of replacing diverse stocks with more uniform breeds or strains. The object of general investigations of breeding is to learn the best methods of producing uniform strains of domestic plants and animals and of preserving uniformity through many generations.[2]

The tendency to look upon uniform expression of characters as the normal condition of heredity is reflected in the terms that have been proposed for the designation of uniform groups of plants or animals, such as "pure race," "pure line," "elementary species," "biotype," and "genotype." Though proposed in connection with different theories, these words all have reference to the idea of heredity as naturally fixed and definite, as shown in uniform groups or series of individuals. The existence of normal species of diverse interbreeding individuals is disregarded.[3]

---

[1] Pearl, Raymond. Some Recent Studies on Variation and Correlation in Agricultural Plants. American Naturalist, vol. 45, no. 535, 1911, p. 415.

[2] Cook, O. F. The Superiority of Line Breeding over Narrow Breeding. Bulletin 146, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1909.

[3] The word "genotype," which several writers on heredity have adopted recently from Johannsen, is objectionable from the standpoint of systematic biology because it was already in use to designate the specimen or species that serves as the type of a

In cotton, and doubtless in other open-fertilized crops, a breeder sufficiently familiar with the peculiarities of his type can maintain a higher degree of uniformity by roguing out the aberrant plants than by the use of progeny methods, with roguing neglected. The uniformity of the Triumph cotton, as maintained by the originator of the variety, Mr. Alexander Mebane, at Lockhart, Tex., was found, some years ago, to be greater than that of any of the varieties that had been developed by the use of the progeny rows. Strictly speaking, the pure-line or pedigree method of breeding is not applicable to cotton in actual practice. The methods of selection that have been worked out for wheat and other self-fertilized types can not be expected to produce the same results with open-fertilized plants like cotton. If the parent plants are not selected with care as representatives of a single varietal type, the crossing that takes place in the progeny rows is the same as when different varieties are planted together for comparison and testing. Nobody would seriously propose to save the seed of such plantings with the idea of securing pure stocks. Without strict adherence to the varietal type, the progeny-row method is not only unable to produce uniform varieties of cotton, but is more likely to maintain diversity of continued crossing. If a plant has been selected because of any divergence from the varietal type, the seed ought not to be grown in the same block with the progenies of plants that represent adherence to the type. In other words, variations and progenies should be recognized as different kinds of material and kept apart. The breeding of new varieties by the selection of superior variations is a task quite different from that of preserving the uniformity of superior strains by selecting for close adherence to type. Varieties are originated by preserving variations, but are preserved by rejecting variations.

A thoroughly uniform variety represents a complete suppression of the normal diversity or heterism usually to be found among the members of natural species. Though differences due to external conditions should not be allowed to interfere with the recognition of uniform groups, there is a practical necessity of placing the members of a group as nearly as possible under the same conditions if uniformity of expression is to be judged. The basis of selection to maintain uniformity is not a mere ideal type or artificial standard estab-

genus, as proposed by Schuchert in 1897. (Science, n. s., vol. 5, p. 639; see also Bather, F. A., Science, n. s., vol. 32, Dec. 30, 1910, p. 953.) The following new definitions have been offered recently by Dr. G. H. Shull: "Genotype, the fundamental hereditary constitution or combination of genes of an organism." "Biotype, a group of individuals possessing the same genotype." "Pure line, a group of individuals traceable through solely self-fertilized lines to a single homozygous ancestor." In an earlier paragraph is the following explanatory statement regarding pure lines: "There is another prevalent misconception regarding 'pure lines' to which attention needs to be called. The word 'pure' in this connection does not refer to the genotypic equality of the individuals, but only to the exclusion of all crossing as a source of genotypic differentiation." (See Science, n. s., vol. 35, Jan. 5, 1912, p. 28.)

lished by score-card reckonings of the values of different characters, but is an actual, visible type, represented by the normal members of the variety as they exist in the same field. Familiarity with the variety is therefore to be considered as the first qualification for undertaking the work of selection or roguing to maintain the uniformity of a select strain.[1]

As the expression of the characters varies with conditions, each field of cotton may need to be judged by a standard of its own. Even in parts of the same field, plants that belong to the same uniform stock may show considerable differences that prevent the application of any absolute standard, except the standard of uniformity itself. Every plant is to be rejected that shows any sign of being different from its neighbors. Superior variations need to be removed, no less than inferior variations.

This method of preserving uniform varieties by rejecting all deviations from the type has often been confused with mass selection but is essentially different. Mass selection simply preserves individuals or lines of descent that show one or more desired characters in a special degree, without requiring that such superior individuals shall conform in other respects to a definite varietal type. The object of conservative or agronomic selection is not to originate or to improve varieties but to maintain the uniformity of superior strains already separated. It is worth while to compare this form of selection with others and to consider their relations to uniformity of expression. The different forms of selection may be described briefly as follows:

Natural selection represents an irregular and usually a partial application of many standards. Adverse conditions are not applied equally or at the same time to all the members of a natural species. The result of natural selection is to discriminate against individuals and lines of descent that are inferior with respect to the various requirements of existence under natural conditions, but such selection would not be expected to develop a state of uniform expression of characters.

Mass selection involves a more consistent application of one or more standards of superiority, but without reference to uniformity in other respects. The result of mass selection is to secure a higher average of expression of desired characters, but without establishing any general uniformity by the separation of the families or lines of descent that have the most regular expression of characters.

Individual selection goes beyond mass selection by choosing superior individual plants to serve as parents of select strains. It avoids crossing among the descendants of different types of superior indi-

[1] Cook, O. F. Cotton Selection on the Farm by the Characters of the Stalks, Leaves, and Bolls. Circular 66, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1910.

viduals, which is one factor of diversity in groups maintained on the basis of mass selection.

Progeny or centgener selection is a more careful form of individual selection based on comparison between progenies of superior individuals to determine the regularity of expression of characters, the so-called transmitting power of the parents of the different progenies.

Agronomic selection is the rejection of all offspring or descendants that deviate from the standards of the superior parent or progeny group.

As a means of preserving the uniformity of select strains agronomic selection supplements progeny selection and is more effective. Instead of relying entirely upon the progeny or pedigree, the uniformity of the stock is guarded in each generation by inspection of all individuals that are to be used for purposes of propagation, in order to reject any individuals that are inferior or that have varied from the type.

With many domestic animals, and with some plants, it is practicable to renew individual or progeny selection with each generation. But with cotton and similar open-fertilized annual field crops it is much more difficult if not quite impracticable to apply these methods on a sufficient scale to secure select seed in commercial quantities. Hence the necessity in such cases of recognizing agronomic selection or roguing to type as a regular responsibility of every seed grower or farmer who desires to maintain a uniform variety of cotton. And hence, also, the desirability of distinguishing this method of selection, based on the recognition of a definite type, from ordinary mass selection by score cards or other partial standards, without primary reference to uniformity of expression.

The necessity of agronomic selection as a means of preserving the uniformity of superior varieties is not appreciated from the standpoint of theories that look upon uniformity of expression as a natural condition disturbed only by hybridization or mutation. Apart from such accidents, it is assumed that a pure line, once separated, will remain uniform indefinitely. This theoretical assumption is often allowed to obscure the practical necessity of continued selection.

Johannsen's theory of genotypes and biotypes contemplates a condition of absolute fixity of expression, even to the extent that there shall be no heritable differences among the later descendants of the stock. Fluctuations due to differences of environment are admitted, but nothing is supposed to be gained or lost by further selection. If any definite variation can be detected the stock is pronounced impure or a mutation is supposed to have occurred. In view of the fact that no such absolute and permanent uniformity of expression

of characters is secured, even by vegetative propagation, it may be doubted whether this idea of genotypes and biotypes represents anything that has an objective existence. Judged by the standards of the genotype hypothesis all stocks must be considered impure or else subject to very frequent mutation.[1]

By selection of the lines of descent that show the most regular expression of a desired set of characters, relatively uniform groups are obtained, but these are not biotypes or genotypes in the sense of primary or antecedent states of heredity. They are merely incidental or artificial exceptions to the general law of diversity. Their uniformity is no indication of pure ancestry, but merely a result of the restriction of descent to narrow lines or to a single parent, in species capable of self-fertilization or vegetative propagation. Uniform groups secured by special methods of reproduction are not more natural or more typical of the general conditions of heredity in plants and animals than identical twins would be as examples of heredity in the human species. Twins are not more pure of ancestry than normally diverse children born of the same parents, nor do they afford any reason for believing that a race of uniform ancestors ever existed.

There can be no objection, of course, to the study of identical twins or of other uniform groups of animals and plants by any refinement of mathematical methods of investigation, but mathematical elaboration should not be allowed to mislead us regarding the biological nature of such groups. Their suitability for mathematical treatment does not make them types of normal heredity. Instead of being biotypes or genotypes, select strains do not represent the natural state of heredity in which life and generative power are maintained, but an artificial condition of uniformity that leads finally to weakness and extinction.

The theory of genotypes has met with prompt acceptance from mathematical writers on heredity, but this should not be allowed to obscure the biological facts that make agronomic selection necessary. It is natural that mathematicians should prefer to deal with something that appears definite and fixed, something adapted to their methods of elaboration. But there is nothing as yet to indicate that the field of normal heredity presents any such constants as mathematicians desire to discover. The unknown quantities are too numerous and too intricately related to be resolved by any refinement of mathematical analysis. Biological analysis is a necessary preliminary, not only to distinguish the different factors, but to learn something of their relative importance and interrelations.

[1] The statistical evidence offered by Prof. Johannsen as the basis of the genotype theory was reviewed by Yule and pronounced inadequate. (See Yule, G. U., "Professor Johannsen's Experiments in Heredity," New Phytologist, vol. 2, 1903, p. 235.)

As affording more adequate means of describing the results of biological analysis, mathematical precision of quantitative determinations is very important. But mathematical elaboration considered as a method of investigation is as futile as the logical or metaphysical elaboration formerly so popular and now so little regarded. Zeal for measurement is not the same as biological interest and familiarity with the characters or behavior of the plants. Mathematical biologists have, of course, no conscious intention of placing figures before facts, but the method is often allowed to influence the choice of materials used as the basis of inference. Uniform groups represent a mathematical ideal, and this leads to their acceptance as the normal condition of heredity, even in cases where they are known to be an artificial product of the breeder's art.[1]

PHYSIOLOGICAL STANDARDS OF EXPRESSION.

The extent to which a stock will appear uniform from a statistical standpoint must depend largely upon the characters that are chosen and the perfection of the system of measurements. Varieties that have been brought to a high degree of uniformity in some characters may continue to show a wide range of differences in other respects. It is known, for example, that the types of Indian corn selected for uniformity of ear characters often show notable diversity in vegetative characters. The same is true of the sugar beets that have been so persistently selected for high sugar content but with little or no regard to the establishment of uniform types of plants.

And even though the members of a stock express the same set of characters in the morphological sense, different degrees of physiological strength or weakness may be manifested in the more or less vigorous growth of the vegetative parts or in the size or number of seeds. Such differences in vigor or productive efficiency are as likely to be inherited as morphological peculiarities, especially in line-bred stocks. There is no reason to expect that any two lines of descent would represent absolutely the same level of physiological efficiency, though it is to be expected that many lines of a carefully selected stock would agree within the limits of experimental error in testing. In view of the fact that differences between experimental rows of the same stock grown under the same conditions are seldom brought within 5 per cent and often run to 15 or 20 per cent, it is easy to understand that considerable differences may often remain hidden within the range of experimental error. Failure to detect such differences experimentally affords small reason for declaring that they do not exist. Some writers have considered vigor and fertility as

[1] Cook, O. F. Pure Lines as Artifacts of Breeding. American Naturalist, vol. 43, 1909, p. 241.

"unit characters," but even on that assumption the possibility of slight differences would need to be admitted.

The mistake of relying upon pedigrees or upon morphological uniformity of expression of characters as standards of practical breeding is now widely recognized. Selection of superior individuals as parents of pure strains is now based on the physiological standard of actual performance of the progeny, instead of upon ancestry alone. Yet even this refinement affords no complete assurance of maximum yield, for it has been found that the precautions applied to insure the purity of the stock have the effect of reducing the physiological efficiency of reproduction. Instead of remaining equal to the superior ancestor or to each other, pure lines of descent show different degrees of vigor and fertility. Even plants that are propagated from cuttings do not remain forever the same. Breeders familiar with plants like strawberries and potatoes recognize the fact that varieties eventually run out; that is, decline in fertility, vigor, or resistance to disease. A recent writer reports a reduction of the size of the meshes of the network of veins in the leaves in old grapevines and considers this as a phenomenon of senility.[1]

Persistent selection excludes degenerate individuals and lines of descent. The stock is kept nearer to the standard of its best members, but the utmost refinement of pure-line breeding may still fall short of the full possibilities of production. In the very nature of the case a select strain separated from the normal network of descent of the species and artificially excluded from crossing is placed at a disadvantage in relation to vigor and fertility. The physiological value of crossing between different lines, as occurs in the network of descent of natural species, must be taken into account if the vigor and fertility of domesticated plants and animals is to be maintained. This physiological factor of heredity has recently received recognition in connection with the corn crop, as the following statements will show:

> Increased yields are obtained by making the yield of the individual plants more uniform, even when the full possibilities of production are not approached. The best plants of a highly bred variety are not conspicuously more prolific than the best individuals in fields from unselected seed * * *.
>
> Though necessarily impeded by inbreeding, important advances in yield have been made by means of close selection, but the value of these improvements

[1] "Since the leaves borne by cuttings showed but slight increase in the proportion of carbohydrate-producing tissue as compared with those on the original plant, it would appear that vegetative propagation can not and does not produce a young plant. The fact that the normal span of life for woody trees and vines extends in some cases over hundreds of years accounts for the fact that the approach of senility in vegetatively propagated plants is not more obvious. Plants which naturally reproduce by seed will tend to 'run out' after long-continued vegetative propagation, ultimately dying of senility, and it is therefore incumbent upon our plant breeders to develop new varieties from seed to take their place." (See Benedict, H. M., "Senility in Meristematic Tissue." Science, n. s., vol. 35, Mar. 15, 1912, p. 422.)

should not be allowed to obscure the fact that the full possibilities of production are not reached until the increment of vigor obtained by crossing has been added.[1]

Continued selection * * * yielded very promising results with corn during the early years of its application, but the later generations failed to fulfill this promise. Definite reasons for this comparative failure in the corn-breeding work of the United States can now be given, for within the last few years investigators have arrived at some understanding of the underlying principles concerned. These principles are yet but imperfectly understood, but they are sufficiently clear to show that practical corn breeding must undergo a radical change in method if it is to take advantage of the full possibilities which lie open to it * * *. All methods now in use for the improvement of corn are by the application of the selection principle and tend sooner or later toward inbreeding. As corn naturally produces the best results when crossed, we hold that all methods now used are wrong unless combined with some method for continuous crossing.[2]

The neglect of this factor of vigor obtained by crossing is only one of many examples of a general tendency of scientific men to disregard the practical value of any principle or factor that they are unable to explain. Why it is that crossing gives increased vigor is still quite unknown, but the fact has been recognized since the earliest times and has been repeatedly verified by scientific experimenters. Half a century ago Darwin performed many experiments and reviewed a large volume of evidence on the effects of crossing and reached general conclusions which no subsequent writers have overthrown, though such facts have often been disregarded in the discussion of abstract theories. The following statements show the results of Darwin's study:

On the other hand, long-continued close interbreeding between the nearest relations diminishes the constitutional vigor, size, and fertility of the offspring, and occasionally leads to malformations, but not necessarily to general deterioration of form or structure * * *.

These two great classes of facts, namely, the good derived from crossing, and the evil from close interbreeding, with the consideration of the innumerable adaptations throughout nature for compelling, or favoring, or at least permitting the occasional union of distinct individuals, taken together, lead to the conclusion that it is a law of nature that organic beings shall not fertilize themselves for perpetuity.[3]

These opinions were formed in spite of the fact that Darwin was familiar with a few plants that seemed to be specially adapted for self-fertilization. But with his wide knowledge of the organic world, he was inclined to look upon such cases as exceptions and preferred to establish his conclusions on the more general condition.

---

[1] Collins, G. N. The Importance of Broad Breeding in Corn. Bulletin No. 141, pt. 4, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, p. 42.

[2] Hayes, H. K., and East, E. M. Improvement in Corn. Bulletin 168, Connecticut Agricultural Experiment Station, 1911, pp. 3 and 9.

[3] Darwin, Charles. "The Variation of Animals and Plants Under Domestication," vol. 2, p. 159.

Since Darwin's time the biological evidence for the universality of crossing in natural species has continued to increase. The wild types or less "improved" varieties of cereals and other domesticated species have been found to be cross-fertilized. It has also been perceived that even highly specialized adaptations to aid in self-fertilization afford no reason for concluding that the same species does not profit by occasional crossing.

Some species are better adapted than others for maintaining their existence by vegetative propagation or self-fertilization, but it does not appear that any of the higher types of life, either plant or animal, are able to exist permanently without crossing.

The cotton plant is one of many that are adapted for crossing as well as for self-fertilization. In the Egyptian type the stigmas are exserted beyond the stamens and fertilization is more dependent on crossing than in Upland varieties. Here the stigmas are partly immersed among the stamens, so that the opening of the anthers brings the pollen into direct contact with the stigmatic surfaces. That varieties will be found to differ in their ability to tolerate long periods of self-pollination or strict selection is to be expected. Experiments with the artificial self-pollination of Upland and Egyptian cotton do not seem to have furnished any evidence of injury to the later generations of the plants. There is a frequent failure to set seed from artificial self-pollination, but this is also true of artificial cross-pollination. Adverse effects from self-fertilization have been reported recently in Indian cottons.[1]

How the effect of crossing is produced is still as much of a mystery as the other processes of heredity, but the lack of an explanation need not prevent a recognition of the fact, nor of its great physiological importance. The old idea was that inbreeding resulted in some positive injury or poison to the offspring, but from the present point of view we can consider the evil effects as due to an absence of some positive quality necessary for the activity of the protoplasm, some stimulating tension or antagonism that may be aroused by the presence of two kinds of protoplasm derived from different lines of descent. Lack of the stimulation or bracing effect of crossing allows the mechanism of heredity to run down; vigor and fertility decline, and degenerative variations appear.

EXPRESSION REGULATED BY SELECTION.

The benefits of selection must appear greatest in a stock that is declining in productive efficiency. The larger the proportion of small or weak individuals or progenies the greater the contrast with

[1] Leake, H. M., and Prasad, R. Notes on the Incidence and Effect of Sterility and of Cross-Fertilization on the Indian Cottons. Memoirs of the Department of Agriculture in India, Botanical Series, vol. 4, January, 1912, p. 37.

the superior lines that are separated by selection. The rejection of the weaker or more inefficient lines brings the average of the stock back toward the standard of its best members, but it is a practical error to expect that such a standardization of expression will be maintained without further selection. The functions of selection in regulating or stabilizing expression and in preserving the uniformity and productive efficiency of superior stocks is quite as important as that of separating the superior lines to form new varieties.

The separation of a select strain of a plant like cotton is an important agricultural improvement, for it enables a larger crop and a better quality of fiber to be produced. But this does not mean that the strain itself is being improved or placed in a better physiological condition by being kept from crossing with other varieties. There is no reason to suppose that a variety or strain of cotton would last indefinitely, even if it were selected with the utmost skill and persistence. But for practical reasons it is important to know how to preserve select strains in uniform condition as long as possible, so that they can be utilized to the fullest extent for purposes of production. The farmer has the same reason for removing the degenerate plants from his seed field as he has for pulling out the weeds, and a further reason in the fact that the progenies of the good plants will be rendered inferior by crossing if the bad plants are allowed to remain.

A well-bred type of cotton might appear to support the idea that permanent uniformity of expression had been established, if observation were confined to a limited number of plants grown under favorable conditions. But if sufficiently large numbers are examined, or numerous experimental plantings are made in different localities, many definite variations or mutations are likely to be found. From a statistical standpoint such variations may appear insignificant, but they throw light on the degeneration of varieties. In one examination of the Triumph variety of Upland cotton growing under its native conditions at Lockhart, Tex., only three definite variations were detected in about 50 acres. On the other hand, about 2 acres of cotton raised from seed of the Lockhart stock at Kerrville, Tex., showed frequent mutative variations.[1]

If the uniformity of the Triumph cotton at Lockhart had not been ascertained it would have been easy to make the usual assumption that the stock had not been carefully selected, but this theory was definitely excluded by the uniform behavior of the Triumph stock, not only at Lockhart, but in many other places in Texas and other States where very uniform fields of cotton have been grown from Lockhart seed.

[1] Cook, O. F. Local Adjustment of Cotton Varieties. Bulletin 159, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1909.

Some farmers believe that the Triumph stock is especially liable to a breaking up when carried to new localities, though it does not appear that any adequate comparisons have been made with other varieties to determine this point. That such numerous and definite variations should appear in one of the most uniform and carefully selected varieties of cotton is interesting from the standpoint of heredity. It also suggests an important question in breeding, whether there are not natural limitations in uniformity, as well as limitations in vigor and fertility, in varieties that are carefully selected for the expression of a single set of characters.

Renewed assurances of the value of Mendelism for the establishment of pure lines has been given by Bateson in a recent address. The existence of any general tendency to degeneration in pure-bred strains is denied, the possibility of degeneration by failure of expression of certain characters as in albinos and short-jointed forms like the cluster cottons being left out of account. The assumption that all variations must be due to crossing or to incomplete analysis into pure lines is reasserted. The theory is evidently to be retained, even though experimental facts have to be discredited. That degenerate variations show alternative inheritance like Mendelian hybrids is taken to mean that crossing must have occurred. But if it can be positively shown that the variations are not due to crossing, the rogue throwers must constitute a distinct class which can be removed by Mendelian analysis and thus leave a permanently pure stock.[1]

[1] "One of the greatest advances to be claimed for the work is that it should induce raisers of seed crops especially to take more hopeful views of their absolute purification than have hitherto prevailed. It is at present accepted as part of the natural perversity of things that most high-class seed crops must throw "rogues," or that at the best the elimination of these waste plants can only be attained by great labor extended over a vast period of time. Conceivably that view is correct, but no one acquainted with modern genetic science can believe it without most cogent proof. Far more probably we should regard these rogues either as the product of a few definite individuals in the crop, or even as chance impurities brought in by accidental mixture. In either case they can presumably be got rid of. I may even go further and express a doubt whether that degeneration which is vaguely supposed to be attendant on all seed crops is a physiological reality. Degeneration may perhaps affect plants like the potato, which are continually multiplied asexually, though the fact has never been proved satisfactorily. Moreover, it is not in question that races of plants taken into unsuitable climates do degenerate rapidly from uncertain causes, but that is quite another matter * * *. If the rogues are first crosses the fact can be immediately proved by sowing their seeds, for segregation will then be evident. For example, a truly round seed is occasionally, though very rarely, found on varieties of pea which have wrinkled seeds. I have three times seen such seeds on my own plants. A few more were kindly given me by Mr. Arthur Sutton, and I have also received a few from M. Philippe de Vilmorin—to both of whom I am indebted for most helpful assistance and advice. Of these abnormal or unexpected seeds some died while germinating, but all which did germinate in due course produced the normal mixture of round and wrinkled, proving that a cross had occurred. * * * I anticipate that we shall prove the rogue throwers to be a class apart. The pure types then separately saved should, according to expectation, remain rogue-free, unless further sporting or fresh contamination occurs." (See Bateson, W. "Genetics." Popular Science Monthly, vol. 79, no. 4, October, 1911, pp. 319–321.)

No breeder would deny, of course, that varieties or lines of descent differ in the production of degenerate individuals as well as in other ways. This is a feature that is often taken into account in the choice of varieties of garden crops. But this is apart from the main issue whether there are any pure lines of descent that remain uniform in all their members and never throw any rogues. To admit that further sporting is likely to occur is to abandon the claim of permanent uniformity. If the Mendelian doctrine is of practical value, it should be possible to find a permanently uniform pure-bred line of descent in some species of plant or animal, one that could be multiplied to large numbers and subjected to different conditions of existence without sporting.

What the cotton industry needs even more than the breeding of new varieties is the development of a system for preserving varieties from deterioration by removing the rogues as soon as they appear. Whether the object of uniformity is to be attained through the medium of organized efforts of cotton-growing communities, public seed-control stations, or through the activities of private breeders and seed growers, the present need is to educate the public in the importance of uniformity and the need of continued selection as a means of preserving superior varieties. To rely on the Mendelian assurance of securing permanent uniformity by pure line breeding would mean a further postponement of consideration of practical measures that are so obviously needed.

EXPRESSION RELATIONS OF COLOR CHARACTERS.

Though color characters and others that depend directly on chemical reactions most commonly show the Mendelian form of alternative expression, two quite different relations are presented by the color characters of cotton. In hybrids between the Egyptian and the Upland types of cotton the lemon-yellow color of the Egyptian petals usually appears in plants that show a preponderance of other Egyptian characters, but very rarely in plants with distinctive Upland characters. A few hybrid plants, perhaps half a dozen out of as many thousands, have been found with the incongruous combination of Egyptian color with Upland form, but these individuals were infertile and abnormal in other respects. The combination of white petals with Egyptian characters is less incongruous and much more frequent, in some Egyptian fields about one plant in a hundred. Some of the white-flowered Egyptian plants are sterile or otherwise malformed, but many are fertile and apparently normal.

The purple spot at the base of the petals of the Egyptian cotton is inherited in quite a different manner. It is often definitely expressed in hybrid plants with white petals and a preponderance of the other Upland characters, while plants with yellow petals and

the other Egyptian characters may have a very faint spot, or none at all. Unlike the general colors of the petals, which are symphanic with other characters of the same parent and antiphanic to those of the other parent, the expression of the purple-spot character shows a much more indifferent or paraphanic relation with other characters. Even among the conjugate hybrids there is a wide range of variation in the expression of the purple spot.[1]

Nevertheless, the spot character is not without definite expression relations. In a study of the Jannovitch variety of Egyptian cotton from the standpoint of contamination with the inferior Hindi type, some plants were found that seemed to depart from the Egyptian characters only in having the spot of a paler shade of purple than usual. At first this difference was considered quite insignificant, because of the frequent variability of the spot. Even on the same plant there is often a wide difference, some flowers having a well-developed spot and others none at all. But in the autumn it appeared that all of the Jannovitch plants with the pale-spotted flowers produced only small bolls. The recognition of the fact that some of the plants had only pale spots made it possible to learn that such plants also had limitations in the size of the bolls.

The prospect of discovering such a relation by a general system of measurements of spots and bolls would have been very small in spite of the large amount of labor that would have been required. Now that the fact has been recognized, the working out of a mathematical expression of relation between the paling of the spots and the reduction of the size of the bolls might be an interesting mathematical diversion, but it seems quite unnecessary for biological interest or agricultural application. The use of the correlation lies in the recognition of the pale spot as a symptom of degenerative variation or departure from the characters of the Jannovitch type. It affords another means of guarding the uniformity of such stocks by selection.

EXPRESSION RELATIONS OF STRUCTURAL CHARACTERS.

In the Upland type of cotton an abundance of fuzz on the seed is antiphanic to long lint but symphanic with abundant lint. If the selection of Upland cotton be directed exclusively to the production of longer lint, the fuzz tends to disappear and the lint also becomes more sparse. If abundance of lint is to be maintained, selection for length of lint needs to be restricted to plants with fuzzy seeds. The production of fuzz represents a favorable condition for the production of abundant lint. Abundant lint is sometimes found on

[1] Cook, O. F. Hindi Cotton in Egypt. Bulletin 210, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1911, p. 31.

naked seeds, but this is opposed to general tendency and represents an unstable condition of expression. Later generations of naked-seeded selections have shown persistent tendencies to sparse lint in spite of repeated selection to maintain abundance.

The symphanic relation between fuzz and lint does not hold at the other end of the series of variations, for with an excessive development of fuzz the lint usually becomes less abundant. This has been shown repeatedly during the acclimatization of the Kekchi cotton, and the same tendency has appeared in experiments with seed selection in the Columbia cotton. In a series of such selections compared by Mr. Argyle McLachlan the plants that were raised from seeds with a rather thin short fuzz showed a general superiority in lint characters over those raised from seeds with the heaviest coating of fuzz. A new short-staple variety with a very high percentage of lint, recently announced by a Georgia breeder, has unusually short uniform fuzz. Seeds with too much fuzz doubtless represent a partial or complete absence of the normal specialization of the two kinds of hairs on the seed coat.

Long lint is also symphanic with narrower and more pointed forms of bolls and antiphanic to short rounded bolls. A variation toward a more rounded form of boll is seldom or never accompanied by variation toward longer lint, whereas variations toward narrower and more pointed bolls often show longer lint. This relation holds among different species and varieties as well as among individual diversities of hybrids and selected stock. The coherence of these characters is evidently biological and phyletic, unlike the ordinary correlation that exists between abundance of lint and increased diameters of bolls. The fibers do not lie extended in the bolls, but are packed about the individual seeds. It is easy to understand why more abundant lint should involve thicker bolls, but there is no mechanical requirement of longer bolls to contain the longer lint.

The practical importance of the relation between the form of the boll and the length of the lint does not depend upon its being stated in mathematical terms. The breeder has an adequate demonstration of its value when he finds himself able to predict the relative lengths of lint of different plants by simple inspection of the forms of the unopened bolls. In the great majority of cases the shorter lint will be found in the broader and more rounded bolls. Plants with pointed or tapering bolls will sometimes be found to have short lint, but it is much more rare to find longer lint in more rounded bolls.

A statistical statement of the relation would be likely to give no adequate idea of its practical importance, owing to the great variability of the factors involved. The lengths of the lint fibers differ not only on the same plant but on the same seed. Satisfactory measurements of bolls are also very difficult because of the complications

introduced by differences of angularity and taper. The shapes and sizes of bolls differ in the same variety in different places. Even in the same plant the checking of growth by drought may induce smaller and more rounded bolls and shorter fiber. But, in spite of these irregularities, familiarity with the plants usually makes it possible to distinguish at a glance those that show definite deviations from the type of the variety in the direction of more rounded bolls and shorter lint. If elaborate measurements were required to distinguish the variations, the relations of expression would have no practical value in the work of selection.

Another general relation of coherence in the expression of characters in cotton exists between the length of the lint and the number of carpels or locks in the bolls. The Sea Island, Egyptian, and other long-linted types of cotton have fewer locks than the short-staple Upland varieties. The long-staple cottons have three or four locks, but in short-staple cottons a considerable percentage of 5-locked bolls is a regular feature. The same relation is found in hybrids between long-staple and short-staple cotton. Egyptian-Upland hybrid plants that have any 5-locked bolls seldom have long lint, a fact first remarked by Mr. Rowland M. Meade. Likewise among variations of Upland cotton, plants with longer lint generally show smaller proportions of 5-locked bolls.

An analogous relation in the expression of characters not directly connected or commensurable with each other has been reported by Worsley in Capsicum pepper. It was found possible to judge the taste of the fruits from their size and shape. Worsley says:

> I do not claim to have tasted every variety of alleged species of Capsicum, but I have tasted a great number, and I have invariably found that the "hot" tasting properties associated with cayenne pepper are confined to those Capsicum fruits which have pointed apices, the degree of heat varying inversely with the size of the fruit, the smaller being the hotter. Conversely, those fruits with blunt apices are known as "mild" Capsicums, and among these mild fruits the degree of mildness varies with the size, the largest being the mildest.[1]

TWO CLASSES OF HYBRIDS.

The literature of heredity abounds in general statements regarding hybrids. Some writers hold that hybrids are more variable than the parent stocks and others that they are more uniform; some that hybrids are more vigorous, others that they are weaker. But all such generalizations are misleading for the reason that there are two distinct classes of hybrids, governed by different physiological principles inherent in the very nature of the reproductive processes.

Instead of revealing the existence of character units or determinant particles, the study of the formation of germ cells has

[1] Worsley, A. Variation as Limited by the Association of Characters. Journal, Royal Horticultural Society, vol. 36, pt. 3, May, 1911, p. 599.

thrown light on another side of heredity by making it possible to understand the sharp contrasts so frequently found between the first generation of hybrids and the later generations. The cytological discoveries of recent decades have given an entirely new view of the process of conjugation.

Instead of being concerned merely with the union of the germ cells, conjugation has to do with the entire life history of the new organism. Its function is not merely to cause growth to begin but to conduct the whole course of development. The process of conjugation that begins with the union of the germ cells does not come to an end until the new generation has reached the stage of forming its sex cells. It is only the reproductive tissues that can be said to pass through conjugation and go back to the state of simple cells. All the cells that compose the bodies of the higher plants and animals represent specializations of double, conjugating cells, formed by the subdivision of the original double cell or zygote.

In other words, the so-called first generation of a hybrid develops while the conjugation begun by the union of the germ cells is still in progress. What is called the second generation is really the first that represents the results of a complete conjugation. In recognition of these differences the first generation, developed before the original conjugation is completed, has been described as the conjugate generation, while the generation formed by germ cells that have passed through conjugation has been called perjugate.[1]

The results obtained with hybrids in the first generation afford no indication of what is to be expected in the later generations. Nothing could appear more deceptive than the behavior of the first generation of hybrids, until it is recognized that the later generations represent an entirely distinct biological phenomenon. Failure to recognize the fundamental differences between the generations of hybrids is responsible for many vain efforts in breeding.

Conjugate hybrids of cotton are not only much more vigorous than the parental stocks but usually more uniform and more productive, thus arousing lively hopes of developing superior hybrid varieties. But in the perjugate generations none of these promises are fulfilled. The uniformity of the conjugate generation gives place to a multifarious diversity. Many plants are weak and sterile, and many others produce only short and inferior lint. For reasons to be explained in later chapters there seems to be little prospect of breeding hybrid varieties to be propagated by seed. To enable the superior conjugate hybrids to be used for purposes of production will require the development of special methods of producing the seed or methods of vegetative propagation.

---

[1] Cook, O. F. Mendelism and Other Methods of Descent. Proceedings, Washington Academy of Sciences, vol. 9, July, 1907, p. 195.

INTENSIFIED EXPRESSION OF CHARACTERS IN CONJUGATE HYBRIDS.

In addition to different combinations and intermediate degrees of the parental characters, hybrids often show a much wider range of expression, beyond either of the parent varieties. In such cases the characters may be described as extraparental, or outside the parents, instead of interparental, or between the parents. Two forms of extraparental expression may be recognized. A character shown in a higher degree than in either parent stock may be described as intensified. A character that disappears or is expressed in a less degree than in either of the parents is said to be suppressed.

One of the most frequent examples of intensified expression in cotton is the appearance of a bright-green color in the fuzz of hybrid seeds even when the parents show only a slight trace of colored fuzz or none at all.[1]

Other examples of extraparental expression are afforded by the nectaries of the involucre of the cotton plant. The full number of nectaries is three, though their occurrence is usually very irregular in both the Upland and the Egyptian types of cotton. But among the hybrids some plants are found with a full complement of three nectaries on all of the involucres, while other plants have very few nectaries or none at all.

The lint characters of hybrids also show intensification beyond the parental standards. In hybrids between Egyptian and Upland cotton there is not merely a dominance of the long-lint characters of the Egyptian parent, but the hybrid lint is usually distinctly superior in length and strength to the lint of Egyptian cotton grown under the same conditions.

The hybrids differ from the parent stocks in having a greatly increased constitutional vigor, as well as in details of expression of the various characters. This increased vigor is manifested both in the larger size of the hybrid plants and in their greater ability to withstand unfavorable conditions that would restrict a full expression of the lint characters in the parental types. It is conceivable, therefore, that the greater length of lint in the hybrids may be due to their increased powers of adaptation to adverse conditions rather than to any more special change of the lint characters.

It has been noticed that the inequality of lint between hybrids and Egyptian plants is greater under very adverse conditions and less under more favorable conditions. This is in agreement with the general fact that the increased vigor and fertility of the hybrid plants is

[1] Cook, O. F. Reappearance of a Primitive Character in Cotton Hybrids. Circular 18, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1908. See also Suppressed and Intensified Characters in Cotton Hybrids, Bulletin 147, ibid., 1909, p. 8.

more obvious in places where the growth of the plants is restricted. Where conditions favor a very luxuriant growth of the Egyptian cotton the forms of the Egyptian and hybrid plants become more similar, so that it becomes more difficult to recognize and rogue out the hybrids. Under ideal conditions that would permit a full expression of the lint characters of the Egyptian cotton, the length of the lint of the hybrids might no longer appear to be intensified. But if this view be taken, a very high estimate must be placed upon the increased vigor of the conjugate hybrids as a factor of adaptation, for the lint of conjugate hybrids has been distinctly superior to the lint of the pure Egyptian plants in nearly all of the experiments that have been made.

The enlarged nectaries, green fuzz, and many other divergent characters that appear in the second and later generations of cotton hybrids must be considered as representing another form of intensification. They do not appear to be results of greater vigor or more effective adaptation but may be in the nature of reversions. A full development of the involucral nectaries is a less specialized condition than a partial suppression of nectaries. Likewise, many of the primitive, unimproved types of cotton have green fuzz similar to that of the hybrids.

The reversion of hybrids to green fuzz may not involve any very serious disturbance of heredity, if it can be accomplished by a mere suppression of the parental characters. If the relations of the parental characters are antagonistic, so that neither of them can come into expression, the course of development is halted at an earlier stage. It may often be difficult to distinguish between suppression and intensification, for an abnormal development of one character may be due to the suppression of some normal inhibitory adjustment, as shown in the tendency of castrated animals to grow to larger size than normal individuals. Thus, a result which in some cases is due to increased vigor may arise in other cases from sterility or some other abnormal condition. The expression of one character represents a condition, favorable or unfavorable, for the expression of another, each character representing a stage in the sequence of development.

That hybridization often has the effect of inducing wholesale reversion or reappearance of ancestral characters has been recognized in such well-known cases as the blue hybrids produced by crossing two white varieties of pigeons, the redder plumage of hybrid fowls, and the reappearance of the incubating instinct in crosses between two nonsitting varieties. Such atavistic reappearances of more primitive characters seem to be almost as frequent as other methods of adjusting the expression relations of contrasted parental charac-

ters in hybrids, and as worthy of being taken into regular account in interpreting the phenomena of hybridization.[1]

DEGENERATION IN PERJUGATE HYBRIDS.

The utilization of the increased vigor and fertility of hybrids is a difficult problem because the intensified condition is only temporary. Hybrids between Upland and Egyptian cotton are often very uniform in the first generation, as uniform as the parent stocks, or even more so. But in the second and later generations this uniformity disappears and is not recovered. For three or four generations some individuals continue to show resemblance to the superior first-generation hybrids, but progenies of such plants are diverse, like those that are obtained from the so-called heterozygotes in a typical Mendelian hybrid. The other plants that correspond roughly to the homozygotes of Mendelism return to the expression of the characters of the parental stocks in different degrees and combinations. In many cases there is an almost complete return to the Upland or the Egyptian characters, but such "extracted" individuals very seldom, if ever, attain the parental standards of expression of the lint characters. The Uplandlike plants do not have as good lint as the Upland parent, and the Egyptianlike plants are similarly inferior to the Egyptian parent.

All of the plants that have been selected for the desired combination of Upland vegetative characters and Egyptian lint characters have yielded utterly diverse progenies. In some of the best progenies detailed comparisons were made to see whether any of the desirable individuals were alike, but without finding even two of them with any close similarity in external characters.

In addition to the hybrids that might be supposed to correspond to the Mendelian classes, another group might be recognized to contain the abnormal or aberrant individuals, those that show extraparental expression of characters. Such deviations appear in many organs of the plant, if not in all, including the habits of growth and the system of branching, the form, texture, and hairiness of the leaves, and in all of the recognized characters of the involucres, bolls, seeds, and lint. Many of the aberrant plants produce very little cotton and some are completely sterile. These abnormalities do not appear in the conjugate generation, where extraparental expression is limited to unimportant details, like the greener color of the fuzz. As already stated, the conjugate generation is usually less diverse

[1] Four general reactions of expression may be recognized in first-generation hybrids. In some hybrids there is a blended or combined (mixophanic) expression of the contrasted characters. In other cases one of the parental characters is suppressed (hypophanic), allowing the opposed character to appear as dominant (epiphanic). When both of the parental characters are suppressed, so that a more primitive character appears, the result may be described as reversive or atavistic expression (palimphanic).

than the parental stocks, while the perjugate generations are much more diverse than the parental stocks because of the presence of the intermediate and extraparental expression of characters.

In the hybrids between the Upland and Sea Island types of cotton made originally by Dr. H. J. Webber and bred by progeny-row methods for about 10 generations, somewhat better results have been secured, either because there is more affinity between the Upland and the Sea Island cotton or because the experiments have been carried on for a longer period. In a series of these hybrids planted at San Antonio, Tex., in the season of 1911, the uniformity was sufficient to show some general consistent differences between the progenies, both in habits of growth and in lint characters. There were none of the very abnormal or completely sterile individuals that often appear among the Egyptian hybrids, yet none of the progenies showed any such uniformity as would be demanded in a commercial variety. The lack of uniformity was particularly apparent in the lint characters. Moreover, the lint no longer showed any advantage from crossing with the superior Sea Island cotton. It was distinctly inferior to that of some of the Upland varieties planted in the same place.

The contrast in behavior between the first generation of hybrids and the later generations shows that two different factors or results of hybridization must be recognized. The vigor or increased efficiency of expression in the first generation is followed by a reaction toward weak or inefficient expression in the later generations. These not only fail to maintain the superiority of the first generation, but fall below the standards of the parent varieties.

One way of describing the results is to say that hybridization undoes the work of selection. The uniformity of expression established in parental stocks by selective breeding is lost, and there is a return to an ancestral condition of indiscriminate diversity. But even this may not represent the entire possibilities of change, for many of the aberrant features shown in the second and later generations of hybrids lie far outside the range of the parental characters, and some of them are so abnormal that they can hardly be taken as simple reversions.

One of the most frequent abnormalities is an enlargement of the involucral bracts. This might be considered as a return to an earlier state when these organs were less specialized. Enlargement of the bracts is frequently accompanied by abortion of bolls. The difference between the fertile and the sterile involucres is often apparent on the same plant. Two involucres of a perjugate (second generation) hybrid between Mit Afifi Egyptian cotton and the Willet Red Leaf variety of Upland cotton are shown in Plate II, right-hand figures (*B*). The enlarged sterile involucres were borne on longer pedicels

and were of a lighter and more greenish color, while the small involucres that produced bolls retained the deep reddish purple color of the Upland parent. A similar inequality in the size of the bracts and the elongation of the petioles was found in another perjugate hybrid between Mit Afifi and Triumph, as shown in the left-hand figures (*A*) of Plate II. In this case there was no difference in color, but the enormous development of the bracts of the sterile involucres, with their coarse texture and long incurved teeth, afforded a striking contrast.

If these abnormalities be considered as examples, intensification may be said to abound in the later generations of hybrids as well as in the first. But in the later generations intensification is no longer accompanied by increased vigor and fertility. It is more often combined with weakness and sterility. The vigor of hybrids does not seem to depend merely on the fact that different characters are present in transmission, but rather on some factor of tension or stress involved in the expression of divergent or contrasted characters. It is easy to understand that the expression relations of the characters would not be the same in the first generation, before the protoplasm derived from the diverse parents has completely united, as in later generations. after the protoplasm has passed through one or more complete conjugations. To make the heterozygote class of the second generation equal to that of the first it would be necessary to assume an absolutely complete segregation of the characters which even the typical examples of Mendelism do not indicate. The final result of crossing the different types is not a constructive improvement or combination of characters but a destructive disturbance of the normal processes of heredity.

It is true that natural species are often found with characters more or less intermediate between those of other species, and many writers have inferred from this fact that hybridizing is one of the natural means of producing new species. But there is very little in the way of direct evidence for the production of new species or even stable varieties by hybridization. The few cases where apparently constant forms have been secured by crossing different species are more reasonably ascribed to peculiarities of reproduction such as parthenogenesis, polyembryony, or amitapsis, or to the exclusive survival of embryos that represented certain combinations of characters. Investigators of Mendelian hybrids have reported cases where one of the homozygote classes failed to develop. If both of the homozygote classes disappeared the heterozygotes would be left as an apparently stable intermediate group.[1]

[1] See Castle, W. E., and Little, C. C., "On a Modified Mendelian Ratio among Yellow Mice," Science, n. s., vol. 32, p. 869.

When hybrids do not breed with each other but are allowed to cross back on one of the parental types the effects of degeneration are not so obvious. The degenerative tendencies that are manifested when the hybrids are bred among themselves are partly counteracted by the effect of the stimulation obtained by crossing with a pure type. This difference was noticed many years ago by the German botanist, Berthold Seemann.

In writing of the inhabitants of the Isthmus of Panama, Seemann made the following statement:

> They [the half-castes] are weak in body and are more liable to disease than either the whites or other races. It seems that as long as pure blood is added the half-castes prosper; when they intermarry only with their own colour they have many children, but these do not live to grow up, while in families of unmixed blood the offspring are fewer, but of longer lives. As the physical circumstances under which both are placed are the same, there must really be a specific distinction between the races and their intermixture be considered as an infringement of the law of nature.[1]

Similar results have been secured in a series of experiments with dilute cotton hybrids. When a pure type, Egyptian, Hindi, or Upland, is crossed with a hybrid the resulting progenies are much more diverse than the first-generation hybrids between the same types. Plants representing only one-quarter of Upland or Hindi blood and three-quarters Egyptian often depart more widely from the normal Egyptian characters than any of the half-blood hybrids in the first generation. The tendency to intensified or extraparental expression of characters in second-generation hybrids is also manifested among the dilute hybrids. Taken as a whole, the dilute or quarter-bloods produced by crossing the hybrids back on one of the parent stocks are distinctly superior to the second generation of the hybrids. At the same time they are distinctly inferior to first-generation hybrids because of the many aberrant individuals. Their status may be described as intermediate between the first generation of ordinary hybrids and the second generation.

If it were necessary to breed from the hybrids, it would evidently be better to combine them with the parent varieties than to breed them with each other, as Seemann inferred. With cotton, however, there is no occasion to use hybrids for breeding in view of the fact that the later generations are inferior to the first. By crossing hybrids of the second or later generations back on one of the parent stocks it might be possible to secure some superior individuals, perhaps as good as first-generation hybrids, but the greater diversity would bring the average far below the first generation. This disparity seems to be less with corn hybrids than with cotton. Nor is it obvious as yet in the series of bovine hybrids produced by Mr.

[1] Seemann B. Narrative of the Voyage of H. M. S., *Herald,* vol. 1, 1853, p. 302, 256

A. P. Borden, of Pierce, Tex., between several American and East Indian breeds.

If it became possible to apply vegetative methods to the propagation of cotton, the dilute hybrids might be worthy of further attention, since they afford a means of combining two of the effects of hybridization—vigor of growth and intensification of special characters. That hybrids may be grown from cuttings was shown at Bard, Cal., in the season of 1911. The plants thus obtained were very vigorous and productive, and the bolls were even larger than those of the overwintered parent individuals from which the cuttings were taken and also larger than those of other first-generation hybrids raised from seedlings, as shown in Plate III. The two bolls at the top of Plate III represent the parent plant, the others a plant grown from a cutting.

INTENSIFIED CHARACTERS IN SELECT STRAINS.

Darwin and many later writers have ascribed to selection a more active power of producing changes of characters than the facts of breeding seem to justify. The improvements effected by breeders are supposed to represent changes of the same nature as those that lead to the evolutionary development of new characters. In reality, however, the analogy is not complete. The difference becomes apparent when the nature of the processes is more carefully considered.[1]

The breeder who works through selection alone does not undertake to change the characters of any particular plant or animal. Selection is merely a way of making use of differences that are found already in existence. The lines of descent that show the highest expression of a desired character are preserved and propagated, the other lines discarded. To replace inferior lines by superior lines is a practical improvement quite independent of any change of characters in the select individuals or their descendants. Selection maintains the expression of the preferred characters at a higher average because the inferior lines are eliminated and no longer figure in the average. Such changes are mathematical instead of biological and afford no reason for supposing that selection has in itself any power to create new characters or even to alter expression. The breeder finds superior individuals and uses them to propagate a superior group. Selective improvement is a process of substitution of groups, not of transformation of characters.

The skill of the breeder lies in his ability to distinguish minute differences and thus to separate more successfully the lines of descent that show the largest and most uniform expression of the desired

[1] Cook, O. F. Methods and Causes of Evolution. Bulletin 136, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1908.

characters. It may be easier to find the desired type by a careful following of the lines of descent than by wandering at random through an endlessly diverse population. The skillful breeder may secure more striking and valuable results with relatively small numbers than less discriminating observers would obtain from much more extensive material. Some breeders begin by hybridizing to induce a wider range of variation than the natural groups afford, but many of the variations shown by hybrids can be found in the parent stocks if a thorough search be made. Hybridizing is of doubtful value with an open-fertilized, seed-propagated plant like cotton, because of the greater difficulty of securing uniform expression of characters after hybridization has occurred.

Without ascribing to selection any direct effect in changing characters, the possibility that some changes may be induced indirectly should be recognized. The methods of propagation that are applied to select groups may be responsible for some of the results that have been ascribed to selection. Selection is usually accompanied by restriction of descent to a few ancestral lines. The range of crossing is narrowed more and more as selection becomes more discriminating and efficient, until the method of pure-line breeding is reached. This calls for the narrowest possible limitation of ancestry, by in-and-in breeding or self-fertilization.

The chief object of restricted descent is to secure a uniform expression of desirable characters in the progeny, but this is not the only effect of narrow or line breeding. The evil results that often arise from consanguineous marriages have been recognized since very early times and by very primitive peoples, and similar results are known to follow with many species of plants and animals. Inbred strains are preserved only by persistent weeding out of degenerate individuals.

Two principal kinds of injury from narrow breeding may be distinguished, though they are likely to be found together. One is a lack of constitutional vigor, usually manifested in smaller size or diminished resistance to disease or to unfavorable conditions. The other is an increase or intensification of any abnormal feature or tendency of the parents.

Any lapse from normal heredity in the parent is likely to be repeated in at least a part of the descendants. Thus, the Arabs of Palestine consider it undesirable to breed from a horse having any of the skin white, however small the area, for they say that the spot is likely to be much larger in the foal. The tendency of any abnormal characteristic to reappear is greatly increased when it is represented in the heredity of both parents, which is more likely to occur when narrow or line breeding is being practiced. Albinism and other

changes of color are among the most frequent of these degenerative variations that appear in groups subjected to narrow breeding.

When one of the degenerate variations of a select stock happens to coincide with an object that is being sought by breeders it is only natural to look upon the result as a direct effect of selection. A seedless apple or other degenerate variation is likely to be hailed as a triumph of selection, even when there has been no attempt to produce that particular variation. The chances of securing such a variation as seedlessness can be increased, no doubt, by propagating from individuals that have fewer seeds, but the increase of the abnormality in any particular individual can hardly be ascribed to selection. The steps have to be taken by the plants themselves, not by the operator. All that can be done is to find a seedless individual and propagate it from cuttings.

The truth is that we have no means of causing any desired variation to appear, by selection or otherwise. All that we can do is to take advantage of the general fact that variations do appear and seek for the most desirable. There are ways of inducing variation by changing the environment, by crossing, or by degeneration through narrow breeding, but these methods do not assure us of any particular result; they only increase our chances of finding what we want. As in throwing dice or dealing cards, the chances are against any particular combination being formed in any limited number of cases. The larger the number of combinations the greater chances that some of them will prove desirable. Selection is the art of finding the combinations after they have occurred, but it is not the art of making combinations. That more desirable combinations or degrees of expression may appear in selected stocks is not to be ascribed to selection, except indirectly, in the same way that the undesirable, degenerate variations must also be considered as results of the condition of inbreeding that selection induces. The undesirable variations are vastly more numerous than those that are superior or even equal to the parental type.

Whether losses of color or of other normal characters represent simply failures of expression or more deep-seated injuries of the mechanism of transmission is not known. The Mendelian inheritance of such variations has been taken as proof of alternative transmission, but alternative expression serves as well to explain the mathematical relations of Mendelism and also accounts for the frequent cases of reversion or reappearances of characters, even after they have been suppressed for many generations. To explain reversion, Mendelian writers have suggested that such characters may be due to two or more factors that have been transmitted separately and then reunited by crossing. But this factorial explanation of latency can hardly be brought into action when reversions take place without

crossing. Recourse must then be had to the idea that the character or factor has been recreated as a mutation.

The fact that so many of the differences between select varieties show Mendelian inheritance may be taken to indicate that the suppression of characters is a very frequent occurrence among our domesticated animals and plants. Similar variations occur, of course, in wild species, but they seem to be much more rare, and seldom able to persist. The white, black, brown, or yellow colors that distinguish the domesticated varieties of mice, rats, guinea pigs, or rabbits, the characters that afford the materials for so many Mendelian experiments, are not paralleled by any corresponding differences among the related wild species. It is the same way with plants. The cultivated varieties differ largely by the absence of some of the characters that all of the wild types have. Thus no wild or unselected stocks of cotton are known to have the shortened "cluster" type of fruiting branches, which represents one of the most frequent of mutative variations of select strains.

The differences that distinguish natural species are not like the sharply contrasted unit characters that distinguish mutations, but are of a much more general and indefinite nature. Nor do hybrids between natural species vary in the same definite ways as hybrids between select, uniform varieties. Instead of merely different combinations or intermediate expression of the characters of the parent individuals, interspecific hybrids generally show a much wider range of variation, both above and below the standards of the immediate parents.

It usually takes several generations of domestication for wild species to break up into various colors and other varietal differences, but when these changes occur they often follow remarkably parallel lines. It is possible, apparently, to secure cluster variations in any type of cotton that is subjected to selection. The same tendency to abnormal shortening of internodes also appears in many other plants, as witness the "bush" varieties of squashes, peas, and beans.

Aberrations of color characters are frequent in plants as well as in animals. They are usually confined to the flowers, though variegated leaves also occur, probably in all the families. Complete albinism is an impossibility among the higher plants, because the albino individuals starve to death in the seedling stage as soon as the supply of nourishment stored in the seed is exhausted. The absence of chlorophyll prevents the formation of starch and thus inhibits development. Yet many albino seedlings have been seen, both in cotton and corn. In such cases it is certain that the variation is not in the nature of a reversion, for no albino ancestor could have lived or produced seed.[1]

[1] That albino plants would be able to live and reproduce like albino animals, if they could nourish themselves, was indicated by an instance, called to my attention, at

It has to be recognized, therefore, that domesticated plants and animals are subject to certain forms of negative variation, representing losses or suppressions of characters. The progressive increase or intensification of a negative, degenerative character under conditions of selection should not be mistaken for a positive, constructive development of a new character. The possibilities of selection are by no means the same in the two cases. Lintless varieties of cotton would be very easy to develop by selection, for all types of cotton show frequent variations toward reduction of lint. Even without any such selection, plants with no lint at all have appeared. All the selective effort has been applied to the increase of the length and abundance of lint, and yet no marked increase or intensification of these characters seems to have occurred. Unselected Mexican and Central American varieties of Upland cotton have lint as long or longer than any corresponding varieties in the United States.

There are hundreds of inferior mutations with short or sparse lint to one that is superior to the parental type, or even equal. Though continued selection is necessary to preserve the uniformity of varieties of cotton and maintain the length of the lint, there is nothing to show that selection can produce further elongation. It is no more reasonable to say that variations toward longer lint are caused by selection than to say that selection has caused the much more frequent variations toward short or sparse lint. If the question were to be decided by an average of the variations in comparison with the parent stock, the conclusion must be that selection has an adverse effect.

The idea that it is possible by dint of selection to induce new variations in any desired direction undoubtedly has served as a great encouragement to breeders. It is responsible for some brilliant successes in finding superior types, and also for some costly failures, where something was sought that perhaps did not exist. If a desired change is in the nature of a suppression or breaking down of a normal coordination or specialization of parts, the conditions of selective inbreeding may be expected to favor the increase or intensification of such a negative or degenerative variation. But if a positive character is required, such as an increase of vigor or fertility, or

Somerton, Ariz., in July, 1909, by Mr. Rowland M. Meade. This was an albino bud mutation of a watermelon vine that grew out into a large branch several feet long, supported, no doubt, by its attachment to the green parent plant. All of the vegetative parts of the albino branch were pure white. The leaves were never fully expanded like those of the normal branches. The albino branch bore a single fruit in October, about 8 inches in diameter and of a short oval form. The rind was a very pale yellowish green, somewhat blotched with slightly darker greenish, but still quite pale. The flesh was pale greenish under the skin and pale pinkish within, with a solid white center. The taste was insipid and disagreeable. The seeds were saved to see whether they would germinate and produce albino seedlings, but were accidentally lost. The presence of the green color in the fruit may be taken to indicate that this character did not cease to be transmitted, though it had failed to appear in any of the vegetative parts of the branch.

the largest expression of some special feature or of a specialized organ or function, the task of selection is to find the superior type and then to maintain a uniform stock by removing all defective individuals. Selective inbreeding seems to intensify only the negative characters. Positive characters are intensified by crossing.

INTERMEDIATE EXPRESSION OF METAMERIC DIFFERENCES.

Abnormalities are of interest in the study of heredity. To understand what happens when the mechanism of heredity becomes deranged is to gain a better idea of the normal processes. Our knowledge of the functions of the internal organs of the human body has been gained very largely through the study of diseased conditions. Many kinds of abnormalities have been described and classified, the study of such phenomena being recognized as a special branch of biological science, called teratology.

One type of abnormality of very frequent occurrence in the cotton plant may be ascribed to an intermediate expression of characters that normally distinguish the different kinds of metamers or internodes that make up the bodies of plants. With many plants a section of the stem with its leaf or leaves may be capable of an independent existence, as in the case of the cotton plant. The change of characters required in passing from vegetative to floral parts is normally quite abrupt. When there are only partial or gradual changes of such characters the results appear abnormal.

In all normal cotton plants the leaves of the fruiting branches and the bracts that compose the involucres of the flowers are entirely different structures, quite unlike in size and shape, as may be judged from a comparison of figures 3 and 4. But cases are often found where the normal specializations of leaves and bracts are not reached and abnormal organs appear, representing intermediate stages between leaves and bracts (fig. 5). In some of the bractlike leaves the petiole is only partly suppressed (fig. 6). It often happens that the two sides are unequally affected, the petiole being suppressed on one side but not on the other. One stipule is united with the blade while the other is separated, often for a considerable distance. Such leaves are often distorted, or even torn, by the unequal growth of the two sides, as in the example shown in figure 7. Sometimes there is a reduction in the size of the leaf without a change of form or texture (fig. 8).

In leaflike bracts the form and texture may be normal, but without a proper union of the parts (Pl. IV). Or the parts may be properly united at the base and yet lack the normal specialization of marginal teeth (fig. 9). Sometimes the middle division, representing the blade of the leaf, is much longer than the lateral divisions that represent the stipules (fig. 10).

Such failures of the mechanism of heredity to maintain the normal contrast between leaves and bracts are usually accompanied by an inability to produce the normal structures of the flower and fruit. The flower buds of abnormal involucres are usually aborted. Sterility seems to accompany an intermediate expression of characters in the parts of the individual plant, as well as intermediate expression in hybrids between remotely related species.

Fig. 3.—Leaf of fruiting branch of Egyptian cotton. (Natural size.)

The whole series of "cluster" varieties of cotton shares the tendency to abortion of the buds. The cluster habit represents a failure of the normal differentiation between the internodes of the fruiting branches and those that form the pedicels and involucres of the flowers. The branch internodes are shortened as well as the floral internodes. The leaves of such branches are more bractlike, while the bracts are more leaflike. Intermediate forms of leaves and bracts are

much less frequent in the Upland type of cotton than in the Egyptian, but sometimes occur (fig. 11). Deeply divided involucres are often met with in cluster varieties (Pl. V).

Though such losses of normal specialization usually occur as definite mutative changes of characters, there are also indefinite variations of the same kind. The outer bract of the involucre often has an intermediate form while the others show the normal specializations (fig. 12). These cases are of interest as evidence of a power of spontaneous readjustment in the mechanism of heredity. A fruiting branch that has produced an abnormal internode may afterwards produce normal internodes. An example of this is shown in Plate VI, which represents leaves from three successive internodes of a fruiting branch of Egyptian cotton. The first leaf is of the normal form, with a 3-lobed blade and small stipules. The second leaf has one of the stipules distinctly enlarged and bractlike, while the blade is simple. The third leaf is like the first, with normal, 3-lobed blade and with the stipules only slightly enlarged.

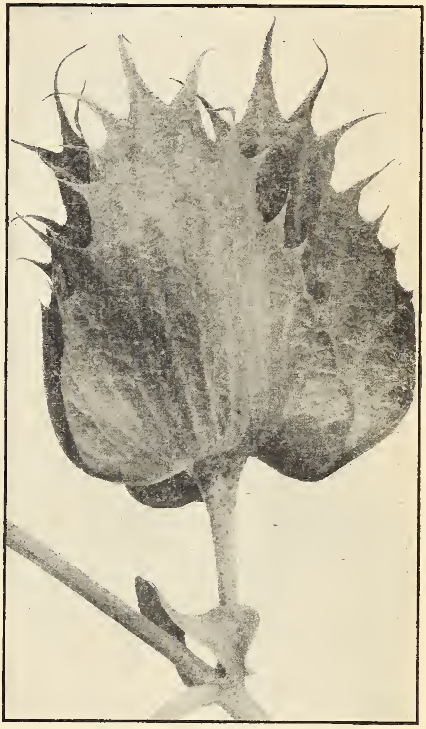


FIG. 4.—Involucre of Egyptian cotton with normal bracts. (Natural size.)

A power of readjustment is also shown when normal flowers, fruits, and seeds are produced in connection with abnormal leaves and bracts. In one Egyptian variety called "Dale," as grown in California, nearly all of the bracts and leaves of the fruiting branches are abnormal. This variety is also subject to wholesale abortion of buds and bolls. Yet most of the plants are able to produce small crops of seed.

Another class of metameric hybrids is shown in intermediate expressions of the characters of the two types of branches. The abnormal fruiting branches, instead of being slender and horizontal, keep a more upright position and become thicker than the others. Such branches usually abort all of their buds. When bolls are produced they are usually small and misshapen and have many abortive seeds. Plants that fail to develop normal fruiting branches have

a more upright fastigiate habit of growth and usually become taller than other plants in the same rows. At Del Rio, Tex., in September, 1911, it was noticed that abnormal plants in the Durango variety usually had greener stems and bracts than normal plants and either coarser or finer teeth on the bracts. But some of the abnormal individuals that had most of the bolls and seeds abortive had longer and stronger lint than normal plants in the same rows. This could be ascribed, at least in part, to the fact that very little fruit was pro-

Fig. 5.—Abnormal bractlike leaf of Egytian cotton subtending a nearly normal involucre. (Natural size.)

duced. Plants that bear a small crop are less liable to checking by drought or other unfavorable conditions.

The occurrence of abnormal branches, internodes, leaves, or bracts is not a matter of scientific interest alone, but is to be considered in selection. It becomes possible to judge by careful inspection of a plant whether its expression relations are definite and well established or liable to vary. Indications of uniformity may be given by the many internode individuals of a plant as well as by the indi-

vidual plants of a progeny row. Thus at Bard, Cal., in the season of 1911, a plant of Egyptian cotton with numerous abnormal bracts but no other obvious divergence from the characters of the Yuma variety was found on closer examination to have seeds much like the Hindi cotton. There was no fuzz, and the lint retained the length and color of the Egyptian cotton, so that it would have been easy to overlook the other differences if the abnormal bracts had not been noticed.

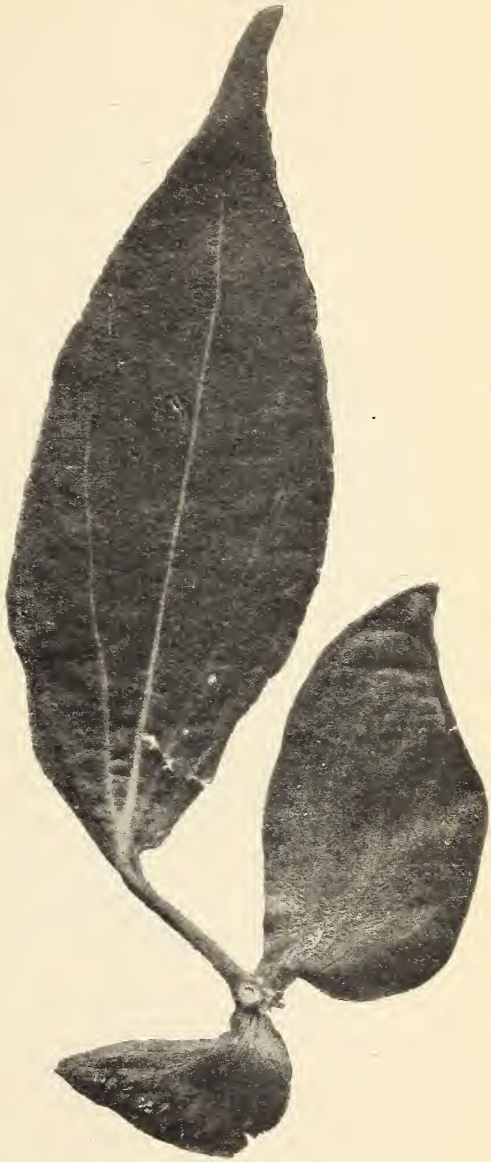


FIG. 6.—Bractlike leaf of Egytian cotton, with the blade and petiole reduced and the stipules enlarged. (Natural size.)

SIMULTANEOUS CHANGES OF EXPRESSION OF DIFFERENT CHARACTERS.

The emphasis given to the idea of characters as independent units tends to obscure another fact of general importance in practical breeding. Independent transmission of characters implies the occurrence of definite variations in single characters, leaving all the other features the same. In reality, such independent changes of single characters occur very seldom, if at all.

The nature of the mechanism of expression is such that a definite change in one character usually involves changes in many other characters. A change of expression does not seem to represent merely a choice among many independent units, but a choice among whole sets of characters

as represented by different ancestral individuals. A close resemblance to a particular ancestor in one feature is likely to be accompanied by resemblances in other features or traits of character. The descendants form a continuation of the ancestral network of descent, sometimes on the same paths and sometimes on intermediate courses. Each plant or animal has its individual characters as well as its individual experience with the environment. As Goethe said: "Nature knows only the individual."

It may be better to think of characters as paths followed by individual ancestors than to attempt to conceive of them as represented by discrete particles existing in the protoplasm. As a species represents a natural entity, because its members breed together in a network of descent, so the characters of the individual plants and animals seem to have a continued existence because of their repeated expression in the lines of descent. The characters are like the threads of different colors that appear on the surface of a woven fabric, only to be lost again as the pattern changes. The same thread returns, but not the same material. The pattern is repeated. but on another part of the cloth. The pattern is only a method of arranging the material. Apart from the fabric itself, there may be nothing to represent the pattern, except the design in the mind of the weaver.

Uniformity among the members of a variety means that each individual follows the same course of development. If any individual wanders from the path with respect to one character it is more likely to continue on a different route during its subsequent development. There is a sequence in the determination of the characters, the expression of one character constituting a more favorable or less favorable condition for the expression of another. With characters standing in such relations to each other, it is easy to see why correlations, coherences, and simultaneous variations should occur. No such flexibility of expression relations would be expected if the characters were independent units, to be varied only by alternative transmission.

That the permanence of ancestral traits should suggest the idea of characters as separate entities is easy to understand on the basis of physical analogies. But notwithstanding the antiquity of the idea of independent character units, no direct evidence of the existence of such entities has been adduced. Instead of being a discovery of modern science this idea may be traced back far beyond Weismann and Darwin to the evolutionary theories of the Sicilian Greek philosopher Empedocles and his Roman disciple Lucretius. These ancient writers described the parts of animals as originating independently and afterwards finding harmonious combinations by a process of gradual adaptation. The idea was doubtless suggested

by the mythical monsters whose existence was credited in ancient times: Centaurs, satyrs, cyclopes, hippocampi, bucephali, etc.

Our modern theories do not contemplate the combination of characters of such radically different types, but they give us no better reasons for holding that characters are separate entities. The ancient and modern theories are also alike in failing to take into account the existence of species, and the normal diversity of members of specific groups. With such an inheritance of diversity it seems to be easier to vary in several characters at once than to change the expression of one character without disturbing the others.

It is convenient for many scientific purposes to describe and discuss characters as though they had an independent existence, in the same same way that navigators treat the lines of latitude and longitude, but the convenience of such analogies affords no assurance of actuality. As well might we expect to find the geographical parallels marked by rivers or mountains. Any analogy that aids investigation is justified by the assistance it affords, but scientific progress is often hampered by holding too long to misleading analogies. It may be that we can form no conception of the workings of heredity without some theory of characters as localized particles, but neither has it been possible to frame any adequate conception by assuming the existence of such particles. To maintain and arrange the particles would require some very effective agency of coordination which no system of independent, separately transmitted units would supply.

Fig. 7.—Bractlike leaf of Egyptian cotton, with the stipule united to the blade and the potiole suppressed on one side but not on the other. (Natural size.)

Whatever may be the cause of simultaneous changes of expression relations, it is of practical importance in agriculture to recognize the fact and use it as an aid in detecting and eliminating variations that would otherwise destroy the uniformity of select stocks. The agricultural value of superior varieties of cotton and many other agricultural

plants depends upon the possibility of maintaining uniformity through many generations. It is quite as important to preserve the uniformity of superior varieties as to develop such varieties in the first place. Indeed, it may be worse than useless to develop and distribute highly selected types of cotton if uniformity is not to be preserved by continued selection, for the degenerate variations of highly bred stocks often fall below the average of ordinary varieties.

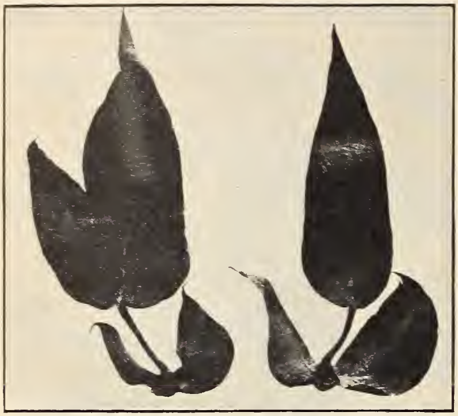


FIG. 8.—Bractlike leaves of Egyptian cotton, reduced in size but only slightly modified in form. (Natural size.)

If each character were at liberty to change independently, the elimination of variations from select stocks would be a well-nigh hopeless undertaking, but the fact that many characters vary together makes it much easier to detect and rogue out the mutations as soon as they appear. For the purposes of Mendelian experiments the existence of varieties differing by only a single character is often assumed, but this has reference to characters with contrasted Mendelian expression, other kinds of differences being disregarded.

The apparent utility of the theory of character units depends largely on the assumption that there are only a few, so that they can all be analyzed by the breeder and separated in pure strains. But in reality the contrasted differences that may be found in a series of hybrids or mutations are extremely numerous. Thus, in cotton there seems to be an apparently endless series of characters that could be formulated on differences of size, shape, position, color, texture, hairiness, and glandular equipment of the various parts of the plants. The largest and most varied series of such differences have been found in progenies of self-fertilized hybrids. According to Mendelian expectations, these should fall into classes characterized by definite distributions of the parental characters, but most of them show characters far outside of the usual range

FIG. 9.—Leaflike bract of Egyptian cotton, with the blade and stipules not completely united. (Natural size.)

of variation of the parental types. Some of the bolls are longer and narrower than in either of the parent types (figs. 13 and 14) and some are shorter or broader (fig. 15). Equally striking variations occur in the involucral bracts. In addition to many other differences of size, shape, texture, color, and marginal teeth, the positions of the bracts are extremely varied. Some plants have the bracts closely appressed to the bolls (fig. 16), while some have them inflated and standing away from the bolls (fig. 17). Another peculiarity is the twisting of the bracts to the side. There is a slight tendency to twisting in the Egyptian cotton, but in some of the hybrids it becomes very striking (fig. 18).

FIG. 10.—Leaflike bracts of Egyptian cotton, with the blade much longer than the stipules. (Natural size.)

Though such hybrids are of no value in themselves, the study of their diversities may aid in the recognition of the less frequent but perhaps equally varied mutations that appear in select stocks. The persistence of the student will determine how many of these variations shall be recognized and described. The descriptive task can be simplified, of course, by confining attention to the extreme forms of variation, but it is no less important to recognize the intermediate members of the series.

In the improvement of the cotton crop, where uniformity of fiber is a primary consideration, the recognition of this principle of simul-

taneous change of expression of many characters is especially important. It enables most of the mutations to be detected early in the season before they have reached the flowering stage. Otherwise they furnish pollen for infecting the seed of their neighbors, with the tendency to degenerate variation. Selection applied at the end of the season is much less effective.[1]

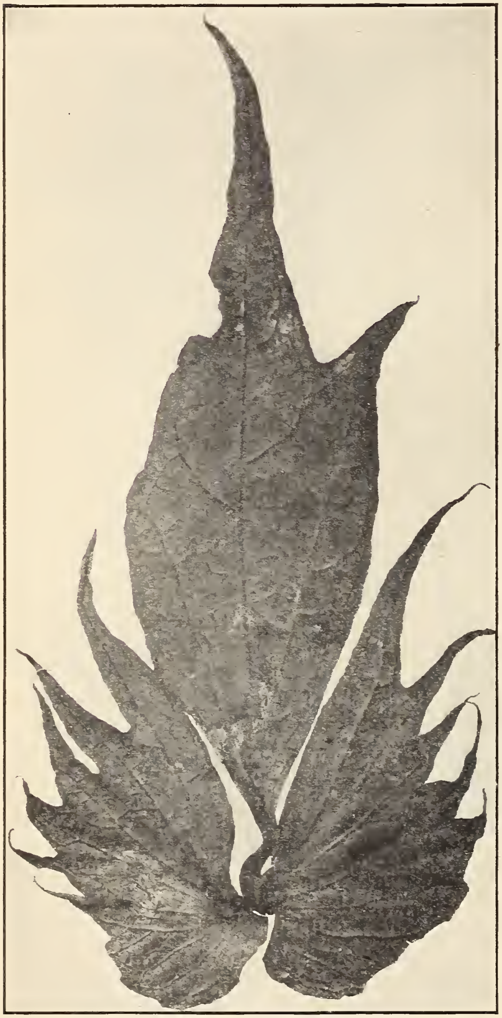


FIG. 11.—Bractlike leaf of Willet Red Leaf variety of Upland cotton. (Natural size.)

Though mutative degenerations can usually be detected by observing the lint and seed characters, it is a much easier method, as well as more effective, to recognize them from the external vegetative characters of the plants. An example of the extent to which mutations often differ from the parent type in lint characters is shown in figure 19, where three seeds from a degenerate mutation are compared with two seeds from an adjacent normal plant in a field of the Lone Star variety at Waco, Tex., in the season of 1911. Though the seed differences are obvious enough when the lint is combed out, this would be unnecessary in actual practice, for the plants that produced the inferior lint could be distinguished from the Lone Star type by simple inspection in the field. For a farmer sufficiently familiar with his variety, the removal of such plants would take no more time than pulling an equal number of weeds and would be much more important for the welfare of the crop.

[1] Cook, O. F. Cotton Selection on the Farm by the Characters of the Stalks, Leaves, and Bolls. Circular 66, Bureau of Plant Industry, U. S. Dept. of Agriculture. 1910.

DIFFERENCES AND SIMILARITIES OF MUTATIONS.

That mutative variations should differ from the parent variety in many respects rather than in only one or two characters is easier to understand when we remember how the condition of uniformity is attained—by the suppression of the normal individual diversity of the ancestral stock. As the mutations that arise in select strains of cotton show the same general range of diversity as the members of unselected stocks, it does not seem surprising that the mutations should differ from each other and from the parent type in many characters, like the individuals of normally diverse groups.

Fig. 12.—Involucre of Egytian cotton, with outer bract of intermediate form and the others nearly normal. (Natural size.)

In addition to a wide range of diversity among the mutations of the same stock, it is also necessary to recognize cases of closely similar or parallel mutations, like those that have been taken by De Vries and other recent writers as examples of evolutionary change in definite directions. Yet there is no reason to expect that mutations, any more than other variations, should differ indiscriminately or show mere random combinations of characters. Observation of many mutations of cotton and other plants indicates that the general laws of correlation or coherence in the expression of the characters apply among mutations as well as among hybrids and among the normal individual diversities of unselected stocks.

As already noted, the single set of characters shown by each of the many members of a variety corresponds to the equipment of a single individual in a normally diverse group, like the human species. Individual men and women do not differ by single characters or by merely random combinations of characters, but show large series of coordinated differences. The fact of correspondence or interrelation between the different characters of the same individual has been recognized by the great French sculptor Rodin, the competence of whose opinions on the characteristics of the human form will scarcely be questioned. In a recent criticism of the method of constructing ideal human forms by combining characters from different models emphasis is placed on the perception of correlations of characters as an essential of artistic ability and taste. Rodin's views are reported as follows:

FIG. 13.—Boll of Egyptian-Hindi hybrid, showing extreme variation toward narrow oblong form. (Natural size.)

> Everything in nature is beautiful for the real artist, for the man of imagination. Nothing is more ridiculous than the effort of an artist to produce something beautiful, something perfect, by combining perfect parts of different models into one. Thus the artist who reproduces the eyes of one model, the hands of another, the feet of a third, the neck of a fourth, produces perhaps a beautiful doll, but it is lifeless and worthless.
>
> There is no such thing as ugliness in nature, in life. Everything is beautiful if seen through the artist's mind. The imperfections become perfect. There is nothing more wonderful than life.[1]

FIG. 14.—Boll of Egyptian-Hindi hybrid, long, tapering form. (Natural size.)

To bring together characters that do not form natural combinations is unpractical for the breeder as well as inartistic for the sculptor. When incongruous combinations of characters occur in cotton hybrids the plants are usually defective or infertile. Many

[1] "Rodin on the Crisis of Sculpture." Literary Digest, vol. 43, no. 4, 1911, p. 139.

attempts have been made to combine the superior lint of the Egyptian cotton with the superior cultural characters of the Upland cotton, but thus far without success. In the rare cases when plants are actually obtained that combine some of the distinctive features of two types, such as Upland habits of growth and Egyptian flowers or Egyptian vegetative characters and Upland flowers, such plants are likely to produce little or no seed.

FIG. 15.—Short, broad form of boll of Egyptian-Hindi hybrid. (Natural size.)

Though mutations and hybrids can often be separated into distinct classes based on the presence or absence of the more definitely alternative characters, they may have a wide range of individual differences in other respects. The diversity manifested in mutations is like the diversity of hybrids, except that the progenies of mutations usually show a much more stable expression of characters. If desirable combinations of characters are found in mutations, they are much more easily preserved than in hybrids. The fact that most of the mutations are degenerate and worthless should not be allowed to obscure the importance of discovering the rare examples of superior mutations to serve as parents of new varieties.

FIG. 16.—Involucre of Egyptian-Hindi hybrid, with appressed bracts. (Natural size.)

Familiarity with the plants gives the practical breeder something that the statistical expert may not have—an ability to recognize desirable plants by direct perception. A skillful breeder has no more need for a score-card system as a guide in selecting a superior plant than a sculptor has for Bertillon measurements in the choice of models.

Most of the mutations of selected varieties of cotton can be described as small-bolled reversions, for they have smaller bolls than the parent variety. Though small-bolled reversions are likely to agree in many other respects, such as narrower leaves, longer inter-

nodes, and more upright branches, they are still very far from being duplicates. When the progenies of such plants are raised each row seems to represent a different variety. Small bolls were doubtless the rule in the ancestral stock from which the big-boll varieties were separated by selection. The persistent tendency of cotton to vary toward small bolls may be compared with that of breeds of chickens to vary toward red feathers or sheep toward black wool or corn toward red ears.

A general tendency for narrow leaves to be accompanied by smaller fruits has been observed among mutations of the coffee shrub in Central America. Planters recognize that the narrow-leaved plants produce a larger proportion of berries with only one seed of the rounded "peaberry" or caracolillo form, which formerly commanded special prices. As might be expected from the tendency to abortion of seeds, the narrow-leaved variations do not yield as well as the parental type of ordinary "Arabian" coffee, and they have not become favorites in cultivation.

FIG. 17.—Involucre of Egyptian-Hindi hybrid, with inflated bracts. (Natural size.)

Another tendency shared by many otherwise different mutations of cotton is toward a shortening of the internodes of the fruiting branches, resulting in the "cluster" type. The shortening of the internodes probably does not represent an ancestral feature or even a positive character at all, but a loss of the normal specialization of parts of the plant, as already stated in a previous chapter. In Mendelian language, this might be described as the absence of a normal or long-joint character replaced by a short-joint character. But the continued transmission of the normal long joint is shown in cases of reversion that appear in cluster varieties, either as individual variations or as modifications induced by environmental conditions.

The inadequacy of the Mendelian theory that mutative variations are caused by a definite addition or subtraction of character units from transmission has been recognized recently by Gates in the case

of a mutation of Oenothera, that gave very frequent reversions to the parent form. The inference is drawn that such changes of characters must be quantitative rather than qualitative. In other words, they can be considered as arising from differences in the strength of the relations that control the expression of the characters rather than because factors of transmission have been added or removed. Gates summarizes his study of this point in the following statement:

On account of these reversions in *O.* [*Oenothera*] *rubricalyx*, which happen in the first and in all later generations, its origin can not be attributed to the loss of a "factor" or an inhibitor or other substance from the germ plasm. The change has been a positive one just as it appears to be. The Mendelian presence-absence hypothesis, commonly used to explain the numerous cases of Mendelian color inheritance in plants and animals, will not apply here. The difference between *O. rubricalyx* and *O. rubrinervis* is instead a purely quantitative one, *O. rubricalyx* having originated through a quantitative readjustment of the materials of the germ plasm leading to the formation of the substances which determine anthocyan formation as a product of the plant's metabolism. This hypothesis is rendered necessary by the fact that these quantitative differences in capacity for anthocyan production are strictly inherited, notwithstanding the well-known fact that this character is subject to wide fluctuations owing to environmental conditions. It is probable that many cases of Mendelian color inheritance are to be accounted for as the result of similar heritable quantitative differences, rather than by the hypothesis of the presence or absence of certain factors in the organisms.[1]

FIG. 18.—Involucre of Egyptian-Hindi hybrid, with twisted bracts.

Selection for extreme earliness and fertility favors abnormal reductions of the vegetative parts. Though such abnormalities would not be likely to survive in nature, they may be valuable in domestication. Under favorable conditions cluster varieties of cotton are extremely productive, but they are easily injured by unfavorable conditions. The crop is often lost by the blasting of the buds, or the quality of the fiber may be injured as a result of premature opening of the bolls.

Thus, the selection of plants that make the very highest yields under the most favorable conditions may defeat the object of securing the most valuable stocks for general purposes of production, just as the persistent selection of fowls with the very highest records as egg

[1] Gates, R. R. Studies on the Variability and Heritability of Pigmentation in Oenothera. Zeitschrift für Induktive Abstammungs und Vererbungslehre, vol. 4, pt. 5, 1911. p. 370.

producers has been found to yield a relatively inferior progeny. The loss of the instinct of incubation in many different breeds specially selected for laying qualities may be compared with the general tendency to shortening of internodes in selected varieties of plants. Nonsitting fowls would be as unsuited to survive in nature as "cluster" varieties of plants.

INTERFERENCE IN EXPRESSION RELATIONS.

The idea that any desired combination of characters can be secured by hybridizing different types of cotton or other plants is in accord

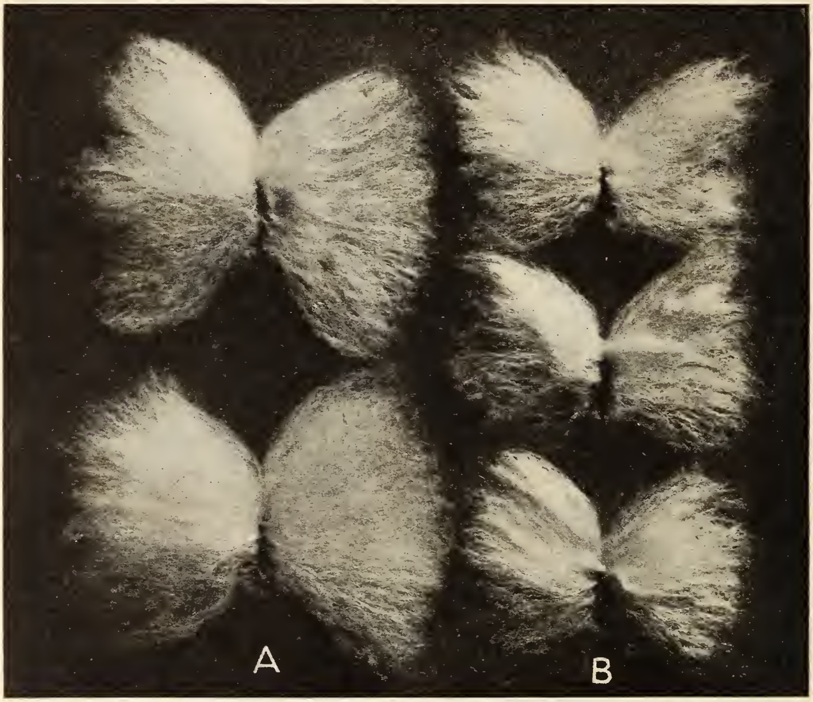


FIG. 19.—Seeds of Lone Star cotton (*A*) and degenerate mutation (*B*), with lint combed out to show comparative length. (Natural size.)

with the theory of characters as independent units capable of separate transmission, but the expression relations are left out of account. In some cases it may be possible to combine two desirable characters in hybrids without interfering with the expression of other characters, but such combinations are often prevented. Strong tendencies to coherence in the expression of a group of characters that have come from the same parent interfere with the substitution of contrasted characters from the other parental group. Thus coherence of characters limits the application of the Mendelian theory of heredity in practical breeding.

That the characters of plants and animals should combine in definite proportions, after the analogy of chemical compounds, is a very attractive idea and is doubtless responsible for the tendency of popular writers to accept assurances based on the Mendelian theory as demonstrated facts. Statements like the following are frequently found in publications on breeding and eugenics:

Pure varieties breeding true can be established permanently by taking into account the Mendelian laws of heredity. Similar results have been accomplished in many other plants and in many animals. A cotton has been produced which combines early growth, by which it escapes the ravages of the boll weevil, with the long fiber of the finest Sea Island varieties. Corn of almost any desired percentage of sugar or starch, within limits, can be produced to order in a few seasons. The hornless character of certain varieties of cattle can be transferred to any chosen breed.[1]

The discrepancy between such an assurance and the actual fact is that the crossing of different types of cotton for purposes of forming Mendelian combinations of contrasted characters does not leave them pure or with the same adjustments of expression of the other characters as before. Though the first generation is often equal or superior to the best members of the parent stocks, later generations are distinctly inferior. The advantages secured by selection are likely to be lost by crossing with a different type. The superiority of selected varieties resides largely in the fact that they show the greatest uniformity in expression of the desired character. When crossing has disturbed this special adjustment of expression relations the superiority of the selected stock is destroyed. Diversity aroused by crossing may serve a useful purpose in furnishing material for a new selection, but this is not the Mendelian idea of forming definite combinations of characters derived from different stocks.

Many of the peculiarities that arise as sudden mutative variations and show Mendelian inheritance are not in the nature of additional characters but represent the absence of normal characters from expression. Hybridization with such variations leads to the subtraction or suppression of characters instead of constituting an addition or positive combination of characters. Mutative variations toward naked, lintless seeds may illustrate this phenomenon in the cotton plant. The lintless character seems to be spreading rapidly in Upland varieties of cotton, especially in the South Atlantic States. The communication of such a negative character by crossing may be much more feasible than the union of two positive characters derived from different stocks, such as the Upland habits of growth and the Sea Island or Egyptian lint.

That mutative suppression of characters is not a rare phenomenon is indicated both in corn and in cotton by the occurrence of albino

[1] Kellicott, W. F. The Social Direction of Human Evolution, 1911, p. 135.

seedlings. As such albino plants never survive to produce pollen or seeds there can be no question that the loss of the green coloring matter occurs quite frequently as an independent variation.[1]

If the superior lint characters of the Sea Island or Egyptian types of cotton could be permanently united with the superior cultural characters of the Upland type of cotton, such as hardiness, earliness, large bolls, and abundant lint, the combination would be valuable. Large numbers of such hybrids have been made, but it has not proved possible to establish their characters by selection. This seems to be prevented by interference of expression relations, as well as by coherence of characters derived from the same parent. Individuals that show definite combinations of the characters of the two types are inferior. Those that show the vegetative characters of the Upland cotton also produce fiber of the short Upland type.[2]

The first generation usually yields better lint than either of the parent varieties, but the later generations are inferior. Perjugate hybrids that have the Upland form not only fail to show long lint like the superior Sea Island or Egyptian ancestor, but usually have very short lint, inferior to that of the original Upland parent of the hybrid stock. The diversities of hybrids, like the mutative variations of selected types, fall into series parallel with the diversities shown in primitive, unselected stocks. In view of the continued transmission of such diversities it is plain that the task of breeding is not to separate the characters in transmission but to understand and control their relations of expression.

An untried possibility of securing more stable combinations of characters derived from different types of cotton has been suggested

---

[1] A recent paper by Worsley recognizes such limitations in the application of Mendelism to hybrids between different species of plants, as the following paragraphs will show:

"When I have followed these hybrid progeny by critical analysis into the second and subsequent generations, I have not been able to satisfy myself that reversion to certain specific characters follows the allegations of the Mendelian advocates. In the first place, I have never been able to find in hybrids any characters that were absolutely dominant or recessive, but have only discerned a certain relative or partial inclination toward the specific characters. Nor have I as yet found a single instance of absolute reversion to either specific type; but I have found that, in the subsequent generations, all sorts of intermediate forms crop up equipoised between the hybrid type and either parent. For instance, if the hybrid type inclined towards the male in colour of flower and towards the female in another respect, I find that some individuals in subsequent generations will do just the opposite, as though the law of change indicated a course of variation which would in time fill up every gap between the two extreme forms represented by the species originally crossed * * *. We constantly find that certain pairs of characters can not be dissociated from each other, but continually occur together in individuals. This association of certain characteristics (so long as it obtains) appears to rule out the possibility of the occurrence of certain conceptually possible intermediate forms. The Antirrhinums give us one instance of this, for among the dwarf self-colored forms every rogue as to height is also a colour rogue, whereas those that are typical in stature will probably not produce 1 per cent of colour rogues." (See Worsley, A., "Variation as Limited by the Association of Characters." Journal Royal Horticultural Society, vol. 36, pt. 3, May, 1911, pp. 596–597.)

[2] Cook, O. F. Suppressed and Intensified Characters in Cotton Hybrids. Bulletin 147, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1909, p. 16.

by a study of diversity. In stocks of Egyptian cotton that have been exposed in previous years to natural crossing some of the lines of descent undoubtedly represent dilute hybrids with Upland or Hindi cotton, in spite of the roguing out of all individuals that showed any definite indication of hybridization in previous generations. Some of the mutative reversions that have appeared in stocks of Egyptian cotton have shown more stable combinations of Uplandlike habits of growth and Egyptianlike lint than any of the hybrids that have been produced artificially.

The suggestion is, therefore, that hybridization may serve as a practical means of inducing mutative variations in desired directions in order to secure more stable combinations of characters than are afforded by the more direct methods of hybridization hitherto employed. Mutative reversions often occur as echoes of previous crossing, even after many generations, a fact very familiar to breeders, but such variations do not appear to have been considered as of possible value from the breeding standpoint. That hybridization is responsible for mutations has often been suggested, even in connection with the original examples of the mutation theory—the forms of *Oenothera lamarckiana* described as mutative new species by De Vries. The recent investigations of Davis are pointing more definitely in this direction.[1]

While none of the mutative reversions toward Upland characters in Egyptian stocks have shown such uniform progenies as some of the mutations that have been found in Upland varieties, no complete uniformity could be expected in view of the fact that the parent individuals have produced their seed under conditions of open pollination. That any considerable proportion of the progeny should express the parental characters and be alike among themselves shows a much more stable condition of heredity than has been found to exist in the progenies of any of the individuals that have been selected from second and third generations of hybrid stocks.

This possibility of inducing mutative variations with desirable combinations of characters also seems to be indicated by facts observed in the Durango cotton. Several years ago many hybrids had been made between the Durango cotton and the Triumph variety of American Upland, in order to combine the larger bolls of the Triumph variety with the longer lint of the Durango type, but this work had been discontinued because no uniform progenies of desirable plants were secured. Many large-bolled, Triumphlike plants had also been selected in the Durango stock, but all these were rejected as probably representing accidental hybrids with Triumph,

[1] Davis, B. M. Genetical Studies on Oenothera. American Naturalist, vol. 45, April, 1911, p. 193.

the variety chiefly grown in the vicinity of the earlier experiments. All of these selections behaved like hybrids in their failure to yield uniform progenies.

Nevertheless, occasional large-bolled Triumphlike plants have continued to appear in the Durango cotton and three progenies raised from such plants at Del Rio, Tex., in 1911, were notably uniform, as though the desired combination of characters had finally been secured by mutative variation from the Durango type. If the uniformity of expression continues, superior strains can be developed from these variations. They have the more upright habit and long lint of the Durango type, together with the larger bolls and more abundant lint of the Texas big-boll type. Two of the large-bolled selections showed another big-boll character, an increased proportion of 5-locked bolls. The percentages of 5-locked bolls in these two cases were 42 and 50, while two adjacent rows representing progenies of typical Durango plants showed only 27 and 29 per cent of 5-locked bolls.

The lint percentage was somewhat higher in the large-bolled selections than in the typical Durango type. Yet there seemed to be no constant relation between the lint percentage and the number of locks in the bolls. Another selection with large Triumphlike bolls gave the highest percentage of lint—36 per cent—though in this case only 21 per cent of the bolls were found to have five locks. This indicates a freedom of combination of the Triumph characters in these induced mutations, much as would be expected in Mendelian hybrids. If such mutations prove valuable, they will afford another reason why breeders should not disregard everything except pure lines.

That the percentages of 5-locked bolls represent significant differences among the Durango selections will be seen from the totals shown in Table IV:

TABLE IV.—*Census of bolls in 5 progeny rows of Durango cotton at Del Rio, Tex.*

Progeny No.	3-locked bolls.	4-locked bolls.	5-locked bolls.	Percentage of 5-locked bolls.	Percentage of lint.
8	0	523	529	50	34
23	5	742	274	27	33
25	1	583	421	42	36
29	0	711	289	29	....
30	2	791	215	21	36

EXPRESSION RELATIONS AFFECTED BY EXTERNAL CONDITIONS.

Expression is influenced by external conditions as well as by internal relations with other characters. That changes of external conditions often result in changes of characters has long been known,

and such facts have often been supposed to demonstrate the possibility of improving plants and animals by direct environmental influences. The question whether nature or nurture has the more important influence in development has been widely debated, often to the neglect of the fact that both are essential to full expression of the normal characteristics of a stock. Unless the substratum of transmission is present and accompanied by the necessary potencies of expression the most favorable conditions are powerless to produce a desired character. On the other hand, the most desirable tendencies may prove ineffective in the presence of too unfavorable conditions.

Many differences in degree of development of characters can be looked upon as standing in a direct relation to favorable or unfavorable external conditions. This interpretation of environmental changes does not always suffice. It often becomes evident that some of the changes must be induced indirectly by environmental modifications of internal relations of expression. Cotton plants of the same strain do not merely grow larger in some places than in others, but change their habits of growth, the form of their branches and leaves, the number of carpels in the bolls, and even the color of the fuzz on the seeds.

The Egyptian cotton has different forms of foliage for sun and shade conditions. At Bard, Cal., in October, 1911, it was noticed that leaves of the main stalk and vegetative branches growing in the sun had at least five distinct lobes and those of the fruiting branches at least three lobes. Under shade conditions the leaves of the vegetative branches had three very broad lobes, while those of the fruiting branches were often simple or without lobes. The last was true especially of the lower leaves produced from vegetative shoots in the latter part of the season when there was more shade.

Changes of branching habits in response to different conditions make it evident that there is no complete determination in advance as to whether vegetative or fruiting branches shall be produced. There is a normal sequence in the production of the two kinds of branches, only the vegetative type being produced from the lower nodes of the stalk, but the change from the vegetative to the fruiting type is subject to adaptive accommodation during the development of the plant.

If environmental changes of characters were merely physiological or quantitative the theory of direct adaptation might be sufficient, but such changes are not confined to characters of environmental utility. Many changes of characters induced by environment are disadvantageous, as when cotton plants show excessive development of vegetative branches and fail to ripen seed.

Recognition of the fact that the plants often change their characters without change of external conditions makes it easier to under-

stand how environmental changes may be brought about. Differences that arise in the same stock of plants under different conditions are subject to the same general interpretation as differences that arise under the same conditions, in that both kinds of differences may be supposed to represent changes of expression relations. The characters that are shown in one place belong to the plants as truly as those that are shown in another place. There are environmental alternatives of expression as well as sexual or Mendelian alternatives. The same nodes on the stalk of a cotton plant will produce fruiting branches under some conditions and vegetative branches under other conditions. In this case, indeed, the same character seems to have both Mendelian and environmental relations of expression, for Leake has announced on the basis of experiments with Indian cottons that the habits of branching are inherited in Mendelian fashion. Special attention has been called to this phase of the subject in a recent address of Prof. Bateson.[1]

The varieties that Leake describes as "sympodial" differ from those called "monopodial" merely in producing fruiting branches lower down on the main stalk. As already indicated, these differences are strictly quantitative and physiological, and are readily affected by external conditions, even to the extent that a plant that would be called strictly "sympodial" in one place will become altogether "monopodial" in another, in the sense that all the fruiting branches are transformed into vegetative branches.

Under current theories of Mendelism the failure of one of the contrasted characters to appear is ascribed to a failure of transmission. On this basis it would not be possible for the same varieties of cotton to show the "sympodial" habit in one place and the "monopodial" habit in another. But the facts stated by Leake may be considered as evidence against the application of the Mendelian theory that heredity is a process of alternative transmission. With expression

[1] "A simple and interesting example is furnished by the work which Mr. H. M. Leake is carrying out in the case of cotton in India. The cottons of fine quality grown in India are monopodial in habit, and are consequently late in flowering. In the United Provinces a comparatively early flowering form is required, as otherwise there is not time for the fruits to ripen. The early varieties are sympodial in habit, and the primary apex does not become a flower. Hitherto no sympodial form with cotton of high quality has existed, but Mr. Leake has now made the combination needed, and has fixed a variety with high-class cotton and the sympodial habit, which is suitable for cultivation in the United Provinces. Until genetic physiology was developed by Mendelian analysis, it is safe to say that a practical achievement of this kind could not have been made with rapidity or certainty. The research was planned on broad lines. In the course of it much light was obtained on the genetics of cotton, and features of interest were discovered which considerably advance our knowledge of heredity in several important respects. This work forms an admirable illustration of that simultaneous progress both towards the solution of a complex physiological problem and also towards the successful attainment of an economic object which should be the constant aim of agricultural research." (See Bateson, W., "Genetics," Popular Science Monthly, vol. 79, no. 4, October, 1911, p. 319; see also Leake, H. M., "Studies in Indian Cotton," Journal of Genetics, vol. 1, September, 1911, p. 205.)

recognized as distinct from transmission there is no reason to deny the possibility that a character expressed in Mendelian fashion among hybrids may also be suppressed or intensified by external conditions. It becomes possible to understand that alternative characters of branches or other organs may remain susceptible to environmental influences as well as to internal relations that govern expression. The influence of external conditions upon heredity has been recognized as one of the most important phases of the subject and one of the most difficult of investigation. An easier approach to such problems is opened by observing the distinction between transmission and expression. The power of the environment to influence the expression of characters can be recognized without assuming that new characters are acquired from external conditions.

In addition to the cases where the expression of characters is definitely limited or modified by the external environment there are instances where expression seems to be only slightly modified or modulated to correspond with the more pronounced environmental changes. If external conditions induce the formation of more rounded bolls a shortening of the lint takes place, just as when there has been a definite change of character, as in round-bolled mutations or reversions. Such differences are sometimes quite clearly marked in parts of the same individual plant. Where cotton plants have been checked by drought and afterwards revived, the "top growth" of previously normal plants usually has smaller and more rounded bolls and shorter lint, similar to those of many small-bolled reversions.

Whether such changes are inherited to any extent through the seed has not been demonstrated by any adequate experiments. There is a general belief that the seed of the last picking is not so good for planting as the seed of the first or second picking. In some cases the first picking is also inferior, owing to the fact that many of the very early bolls are poorly developed and are opened prematurely.

The lint also responds in various ways to adverse conditions of growth. In addition to the general weakness of the lint in prematurely opened bolls, the fiber may also be shortened if the adverse conditions affect the boll in the early stages of growth. Another effect of adverse conditions is to render the lint sparse, as well as short. Sometimes these effects are shown unequally on the different parts of the same seed. The upper end of the seed may have lint of normal length and abundance while the lower end has only sparse or short fibers, aggravating the so-called "butterfly" tendency so frequent in our long-staple Upland varieties.

GENERAL CONCLUSIONS REGARDING THE NATURE OF HEREDITY.

Correct interpretations of the facts of heredity are essential to safe application in practical breeding. The investigator should be able to think correctly about the facts that he observes and to appreciate their relations with other facts. Progress in interpretation lends additional value to the results of investigation, like other improvements in methods of conducting experiments and recording observations.

Heredity includes two distinct processes—transmission and expression. If heredity is to be considered from a mechanical standpoint, two kinds of mechanisms should be recognized, a mechanism of expression as well as a mechanism of transmission.

Transmission is independent of expression and probably includes a complete series of ancestral characters. Characters can be transmitted through many generations in a latent condition, without being brought into expression. The study of many problems of heredity and breeding can be facilitated by more definite recognition of the distinction between transmission and expression.

The differences everywhere found among the members of species of plants and animals are the facts that give practical importance to the study of heredity. Such differences should be considered as variations in the expression of characters, not as variations of transmission. Changes of characters that arise in response to changes of external conditions or to different methods of breeding also represent changes in the expression of the characters rather than changes in transmission.

While it would be a matter of much scientific interest to discover the method of transmission, the practical object of the study of heredity is to learn how to control the expression of characters. Expression is influenced by the mutual relations among the characters as well as by external conditions and methods of breeding. The investigation of expression relations should not be limited to empirical discovery of correlations by measurements of sizes, weights, or colors, but should include a biological recognition of expression relations in unimproved stocks and in hybrids.

The idea that variations represent changes in the expression of characters rather than changes in transmission is in accord with the general manifestation of diversity among the members of natural species and the general tendency of domesticated varieties to revert to the ancestral condition of diversity.

Though the recognition of individual diversity and free interbreeding as normal conditions of heredity conflicts with current theories of descent in pure uniform lines, it is necessary to an appreciation

of the physiological factors of heredity, those that sustain organic vigor and fertility.

The union of the lines of descent of a normally diverse interbreeding species into a network provides for the transmission of all the ancestral characters through all the lines of descent. Undesirable characters are suppressed by selection, but not eliminated from transmission, as shown by the fact of reversion. The function of selective breeding is to secure more regular expression of a desired set of characters. Continued selection is required to maintain the uniformity of superior varieties, because of the persistent tendency of the suppressed characters to return to expression.

The diversity that is aroused by placing a variety under new or unfavorable conditions and the diversity induced by hybridization can both be looked upon as due to the return of latent characters to expression. It is not necessary to assume that new characters are added to the transmitted stock, either by new conditions or by hybridization.

Selection regulates the expression of characters, but is not known to have any influence over the transmission of characters or the addition of new characters to the content of transmission. The evolutionary development of new characters should not be confused with changes in the expression of old characters. Mutative changes of expression are not to be considered as new characters or as examples of the evolutionary progress of natural species.

The normal results of the workings of heredity seen in natural species are not separate lines of uniform individuals but highly varied fabrics or networks of interbreeding lines of descent. Uniform expression of characters, as in line-bred groups, represents an artificial condition of heredity and is accompanied or followed by a decline of vigor and fertility.

Increased vigor and fertility secured by crossing selected strains is to be considered as a result of returning toward a more normal condition of reproduction, like that of natural, freely interbreeding species. It should not be identified with the abnormal vegetative or somatic vigor sometimes shown by sterile hybrids between different species.

Mendelian combinations of characters of different types of cotton are prevented by the fact of coherence. Instead of a Mendelian segregation and recombination, there is a general tendency for characters derived from the same parental type to remain together in expression in the hybrids.

The transfer of a desired character from one variety to another by Mendelian combination of characters may be possible in cases where the desired character is negative or suppressed, but Mendelian com-

binations of positive characters are much less frequent, if they occur at all.

The evolutionary development of new organs and functions involves the addition of new characters to the content of transmission, but such new characters are to be distinguished from variations that represent changes in the expression of characters already present in transmission.

SUMMARY OF APPLICATIONS TO METHODS OF BREEDING.

The practical study of heredity should begin with a recognition of the underlying facts of normal individual diversity and free interbreeding among diverse individuals, as shown in wild species and unimproved domesticated stocks. Uniform expression of characters is not a natural condition of heredity in a cross-fertilized plant like cotton, but has to be secured and maintained by selection.

The effect of propagation from a single parent or in very narrow lines of descent is to establish or stabilitate expression, so that a single set of characters is shown in a large number of individual organisms. Normal diversity is suppressed, but the suppressed characters continue to be transmitted in latent form and return to expression in mutative reversions.

In view of the continued transmission of latent or suppressed characters and the frequent return of such characters to expression, it is not to be expected that selection can be completed once for all by the separation of "pure lines," as inferred from the assumption of normally uniform heredity. In a seed-propagated crop plant like cotton continued selection must be maintained if the uniformity of superior varieties is to be preserved. The value of such selection does not depend on the possibility of securing further improvements, but on avoiding degeneration by loss of uniformity.

The idea that there is a natural uniformity or stability of expression of characters applies to natural species only in cases where special methods of reproduction, such as vegetative propagation, parthenogenesis, and self-fertilization, furnish the same conditions of restricted descent as in domesticated species. Vegetative propagation is the most effective method of securing an unaltered expression of the characters of a selected individual, but even in vegetatively propagated varieties changes of expression sometimes occur.

The establishment of uniform expression of characters involves a departure from the normal condition of free intercrossing between different individuals and lines of descent and an ultimate decline in vigor and fertility. Uniform groups become inferior in these respects to hybrids or to select individuals of unimproved stocks.

The loss of vigor and fertility as a result of descent in narrow lines is to be recognized as a general physiological relation or "law of nature." The result appears much more promptly in some groups than in others, but an ultimate deterioration is to be expected in all. While this fact does not diminish the importance of breeding superior strains of domestic animals and plants, it has important bearings on the choice of methods of breeding, testing, and utilizing such strains. Moreover, it shows the need of providing in advance for the continued development of superior new strains to replace those that have begun to decline in vigor and fertility.

The primitive, wild, or unselected stocks from which our highly selected varieties have been derived ought not to be disregarded or allowed to become extinct on the supposition that they have no further agricultural value. Such stocks may be required at any time in the future as sources of new strains.

It is also important for purposes of practical breeding to take into account the facts of heredity in natural species, in order to learn the best methods of maintaining the uniformity of select strains and of preserving vigor and fertility. Some characters have mutual relations of expression and produce more congruous and more stable combinations. Other characters show distinct incompatibility of expression, resulting in weak or infertile plants.

Comparison of variations in select strains with variations in unselected stocks and wild species of cotton shows that parallel series of variations run through the whole group. Correlations of variations in selected stocks and coherence of parental characters in hybrids seem to follow the same general lines in all the species and varieties of cotton that have been studied from this point of view.

Many of the abnormalities that arise in hybrids and in mutative variations of select strains represent a failure of normal specialization among the parts of the plant, as in the shortened fruiting branches and leaflike involucral bracts of the so-called "cluster" cottons. Such abnormalities are usually accompanied by a tendency to sterility or abortion of buds and bolls and on this account are to be avoided in the breeding of new varieties.

Characters of no practical value in themselves may be worthy of careful study as indications of changes of expression of other characters, as in the case of the paler petal spots that are regularly accompanied by small bolls in the Jannovitch variety of Egyptian cotton. The recognition of degenerative mutations and the preservation of uniformity in superior stocks is rendered much more feasible by the fact that the definite changes in the expression of characters are usually simultaneous. A definite variation in one character is usually accompanied by variations in other characters. Plants that would produce inferior lint can be distinguished by vegetative differences

before the flowering stage is reached, and their prompt removal prevents the distribution of the pollen of inferior plants by insects.

Both in hybrids and in individual variations of selected stocks of cotton there are relations of expression between boll characters and lint characters, so that the nature of the lint can be judged by inspection of unopened bolls and undesirable variations rejected in advance of the harvesting of the crop.

The two color characters of cotton flowers, the yellow of the petals and the purple of the spots, have very different expression relations. In hybrids between Egyptian and Upland varieties the expression of the lemon-yellow color of the Egyptian petals accompanies other Egyptian characters and is only very rarely combined with distinctive Upland characters. The purple base of the Egyptian petals combines much more readily with Upland characters.

Knowledge of expression relations is also required for effective utilization of hybrids of cotton, corn, and other annual crops for purposes of production. The superior vigor and fertility of conjugate hybrids when compared with select parental varieties grown under the same conditions justifies the use of such hybrids for agricultural purposes of production whenever practicable. The increased vigor and hardiness of hybrids is to be considered as a factor of adaptation when it makes possible the production of good crops under conditions too unfavorable to be resisted by the pure-bred parent varieties.

Variations toward Upland or Hindi characters arising in dilute hybrid stocks of Egyptian cotton have been found to yield progenies with more stable expression of characters than direct hybrids between Egyptian and Upland cotton. Such facts suggest the possibility of developing a new method of breeding by dilute hybridization. By the use of a small proportion of foreign blood as a means of inducing mutative variations in otherwise uniform stocks it may be possible to secure desired combinations of characters in more stable form than they can be obtained by direct hybridization.

The deterioration of the later generations of hybrids may be considered as a return to the expression of the characters of more remote and inferior ancestors; in other words, a loss of the potency of expression of desirable characters that was established by the selection of the parental stocks. Thus, the same general result is reached by hybridization as by neglect of selection. There is a return toward the ancestral condition of variable expression of characters.

PLATES.

50600°—Bull. 256—13——7

DESCRIPTION OF PLATES.

PLATE I. Fig. 1.—Kekchi cotton at Bard, Cal., 1911: *A*, Unacclimatized; *B*, acclimatized. The large unacclimatized plant produced only the single boll visible near the base of the main stalk, while the acclimatized plant was heavily loaded with open and unopened bolls. Fig. 2.—Kekchi cotton at Glendale, Cal., 1911. Unacclimatized row at left, acclimatized row at right. In the cooler climate near the coast there were no pronounced differences in the vegetative development of the two rows. The acclimatized stock had somewhat larger bolls and better lint.

PLATE II. Normal and abnormal involucres of perjugate (second generation) hybrids between Egyptian and Upland cotton, showing the larger bracts and longer pedicels of sterile involucres: *A*, Hybrid between Mit Afifi Egyptian cotton and Triumph Upland cotton; *B*, hybrid between Mit Afifi Egyptian cotton and Willet Red Leaf Upland cotton.

PLATE III. Bolls of Egyptian-Upland hybrid: *A*, From parent plant; *B*, from plant grown from cutting. The bolls produced from the cutting were as large as any that have been produced by seedling plants.

PLATE IV. Abnormal involucral bracts of Egyptian cotton, Yuma variety, showing different degrees of specialization and union of the elements that correspond to the blade and stipules of unspecialized leaves. In some cases the stipules are only slightly modified and only slightly attached to the blade. In other cases the specialization is nearly complete, with the parts separated only by a seam or suture instead of being completely fused as in normal bracts.

PLATE V. Involucral bracts of Upland "cluster" cotton, "Jackson Limbless": *A*, Normally specialized bracts; *B*, abnormal, intermediate bracts. Deeply divided involucres are often met with in cluster varieties.

PLATE VI. Egyptian cotton leaves from three successive internodes, *A*, *B*, and *C*, showing variations of blade and stipules. *A* and *C* represent leaves of the normal 3-lobed form, with small stipules; *B*, the intervening simple leaf with one of the stipules greatly enlarged, representing a partial expression of the characters of the involucral bracts. But after producing an abnormal internode the fruiting branch was able to produce other normal internodes.

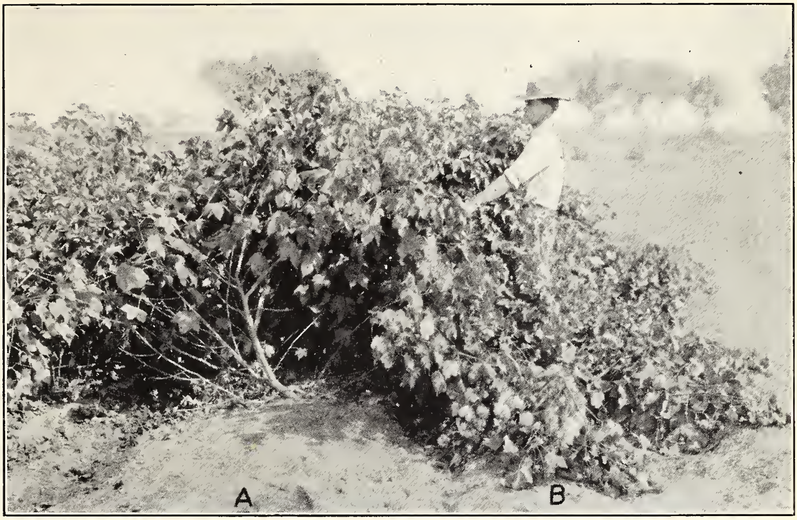
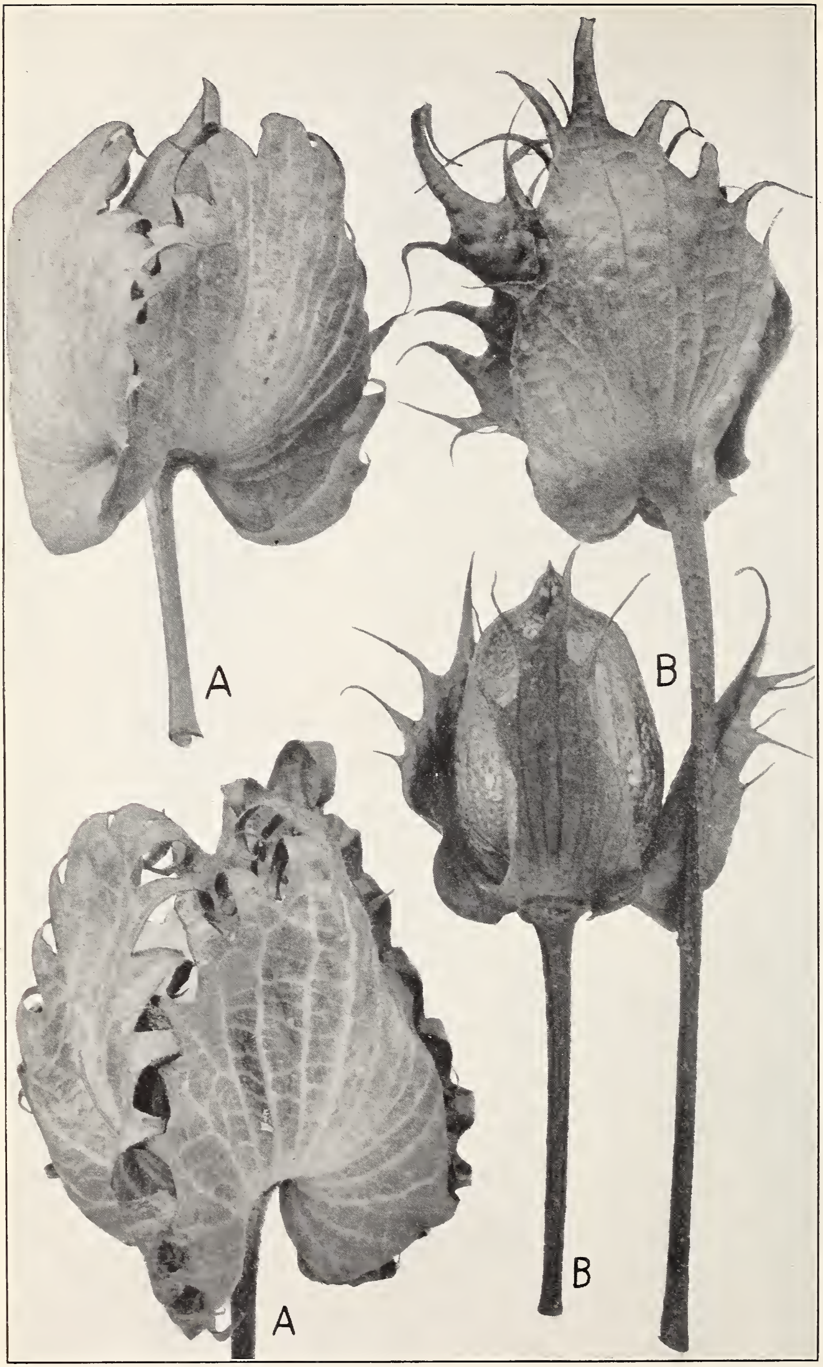


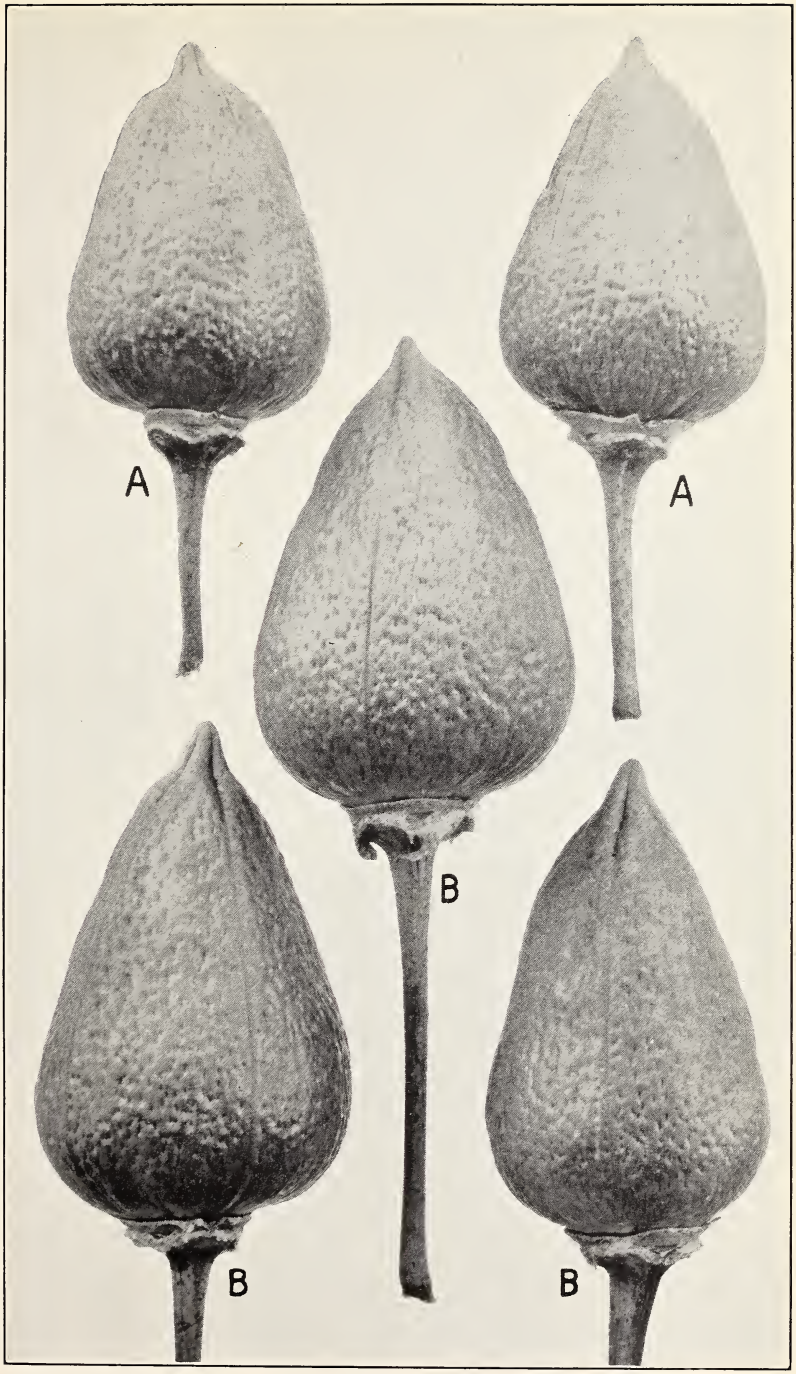
FIG. 1.—PLANTS OF KEKCHI COTTON AT BARD, CAL.: *A*, UNACCLIMATIZED; *B*, ACCLIMATIZED.

FIG. 2.—TWO ROWS OF KEKCHI COTTON AT GLENDALE, CAL.: *A*, UNACCLIMATIZED; *B*, ACCLIMATIZED.



INVOLUCRES FROM TWO PLANTS OF EGYPTIAN-UPLAND HYBRIDS: *A*, NORMAL; *B*, ABNORMAL.

(Natural size.).



BOLLS OF EGYPTIAN-UPLAND HYBRIDS: *A*, FROM PARENT PLANT; *B*, FROM PLANT GROWN FROM CUTTINGS.

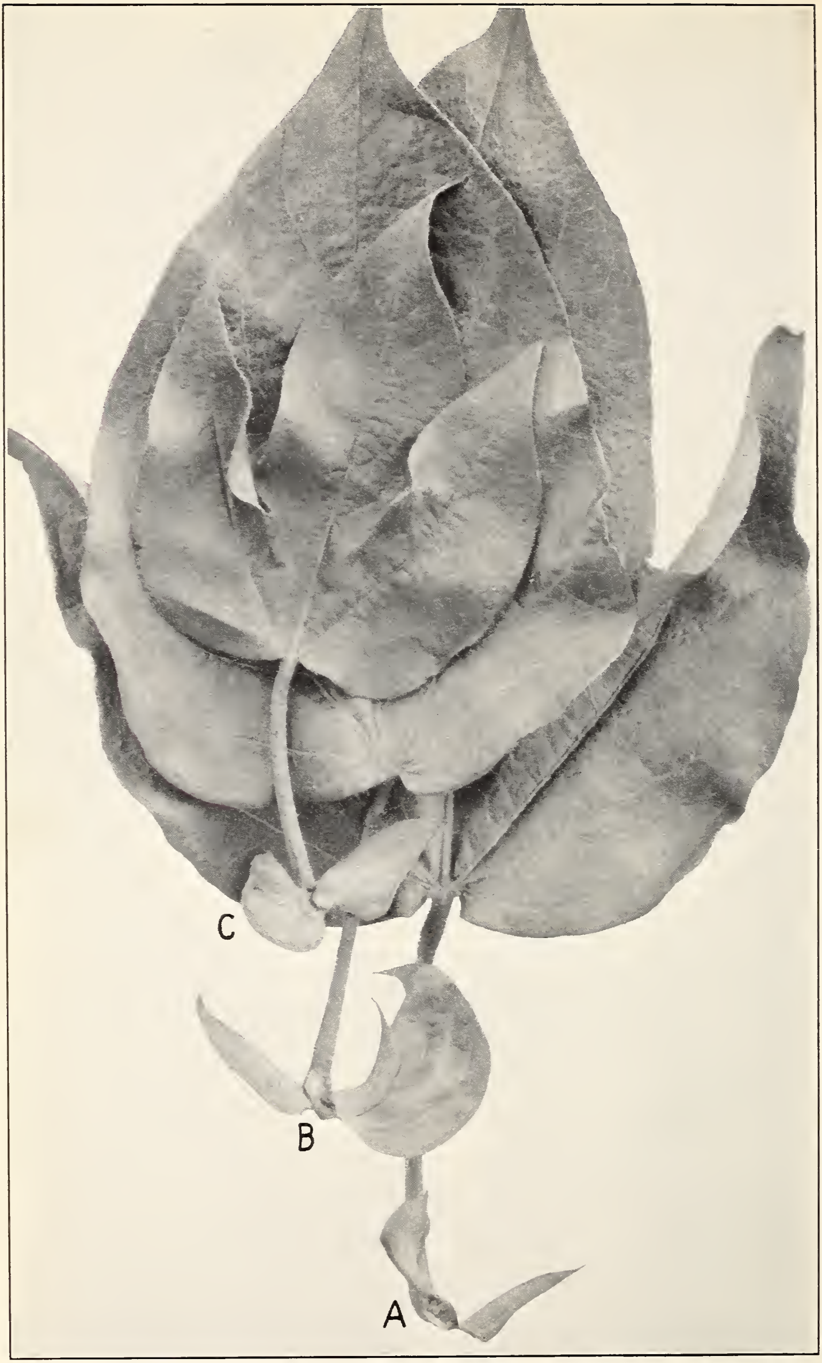
(Natural size.)

ABNORMAL BRACTS OF EGYPTIAN COTTON, WITH STIPULAR ELEMENTS NOT COMPLETELY UNITED.

(Natural size.)

INVOLUCRAL BRACTS OF "CLUSTER" COTTON, "JACKSON LIMBLESS": *A*, NORMALLY SPECIALIZED BRACTS; *B*, ABNORMAL, INTERMEDIATE BRACTS.

(Natural size.)



EGYPTIAN COTTON LEAVES FROM THREE SUCCESSIVE INTERNODES, *A*, *B*, *C*, SHOWING VARIATIONS OF BLADE AND STIPULES.

(Natural size.)

INDEX.

50600°—Bul. 256—13——8